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# ECOLOGY, MORPHOLOGY, AND GERMINATION PHYSIOLOGY OF TREE SEEDS IN A TROPICAL SEMIEVERGREEN FOREST IN THE PANAMA CANAL WATERSHED, WITH SPECIAL REFERENCE TO SEED DORMANCY CLASSES ALONG A PRECIPITATION GRADIENT

Adriana Elena Sautu
*University of Kentucky*, sautuf@cwpanama.net

## ABSTRACT OF THESIS

# ECOLOGY, MORPHOLOGY, AND GERMINATION PHYSIOLOGY OF TREE SEEDS IN A TROPICAL SEMIEVERGREEN FOREST IN THE PANAMA CANAL WATERSHED, WITH SPECIAL REFERENCE TO SEED DORMANCY CLASSES ALONG A PRECIPITATION GRADIENT

The Panama Canal Watershed (PCW) represents a special opportunity for studies related to seed dormancy in the tropics with both applied and basic research objectives. There is a clear need for seed information for nursery planning in restoration projects that involves use of a large number of local species. Moreover, the strong rainfall gradient along the 60 km of continuous lowland forest in the PCW represents an excellent opportunity to understand dormancy and its role as an adaptive trait that evolved in response to environmental factors. This study presents useful seed information for 100 tree species native to the PCW. For each species, it includes collection system, fruiting time, seed mass, seed moisture content, germination, and longevity in storage at 20ºC. For the first time, an attempt is made to classify (to class sensu Baskin & Baskin 2004) the class of dormancy in seeds of the PCW. An analysis of the relationship between class of dormancy and seed mass, moisture content, longevity, germination patterns, and seasonality is presented. The relationship between class of seed dormancy and longevity and geographical distribution of species within the watershed based on the rainfall gradient was investigated.

KEYWORDS: Seed ecology, Seed dormancy, Tropical forest, Precipitation gradient, Seasonality

Adriana Elena Sautu

August 31, 2004

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**THESIS**

**Adriana Elena Sautu**

**The Graduate School**

**University of Kentucky**

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# ECOLOGY, MORPHOLOGY, AND GERMINATION PHYSIOLOGY OF TREE SEEDS IN A TROPICAL SEMIEVERGREEN FOREST IN THE PANAMA CANAL WATERSHED, WITH SPECIAL REFERENCE TO SEED DORMANCY CLASSES ALONG A PRECIPITATION GRADIENT

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**THESIS**

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A thesis submitted in partial fulfillment of the requirements
for the degree of Master of Science in the College of Arts and Sciences at the University of Kentucky

By

Adriana Elena Sautu

Lexington, Kentucky

Co-Directors: Carol Baskin, Ph.D., Professor of Biology and Agronomy
and : Jerry Baskin, Ph.D., Professor of Biology

Lexington, Kentucky

To my mom,
who has sown seeds of love in the classrooms of Argentina
and gave the shade of a giant tree to her family
with no more than tons of faith in humanity.

# ACKNOWLEDGMENTS

To finish a master's degree at the time your children are beginning College is for sure something you cannot do alone. Many years of work with the help of many people and institutions are condensed in the following pages. This thesis is the end of a long journey, and yet I hope it is also another beginning.

My advisors, Carol and Jerry Baskin, said yes to my dream to learn more about the seeds I have been working with for several years. They said yes to me and also to my family, and they continue saying yes to all the distractions involved in a family with teenagers and an artist husband. Carol and Jerry patiently encouraged, guided, and supported my dream and me.

Two American scientists in Panama played a key role in making it possible for me to come to the United States. Richard Condit, Scientific Coordinator for the Center for Tropical Forest Science (CTFS) in Panama, was behind the scenes in all my projects; without him, none of them would have been funded. Mark Wishnie, Director of the Native Species Reforestation Project (PRORENA), did everything possible, both professionally and personally, to push me to the USA and finish the research as part of my graduate work. Georgina de Alba, Beth King, and Julia Velasquez gave me invaluable advice about coming to this country.

Undoubtedly, from all tasks accomplish for this study, the most important, the most difficult, and the most time-consuming was to find the trees and collect the seeds. Two botanists were my "angels" in Panama, Jorge Aranda and Jose Deago. They spent long days driving and walking, with their eyes on the canopy, and they collected thousands of seeds, many of them more than 20 m above the ground. But they would not have been able to do all these tasks alone. All botanists at CTFS, Rolando Pérez, Salomón Aguilar, Agustín Somoza, and Israel Tejada, came to us uncountable times "gossiping" information about some fruiting tree or the places where they had seen this or that species. I say thank you also to Deisa Lamella, who assisted with the organization of everything at the beginning of my studies, and Moises Murillo, who began helping with sand-mixing and seed-cleaning, and ended up being the most complete technician one could expect.

Once in Lexington, I took advantage of the intellectual inspiration of my advisors and from professors such as Mary Arthur, Robert Geneve, and Dennis Tekrony, who was brave enough to serve on my Committee. I also had a pleasurable time in the Department of Biology with my fellow colleagues, and I would like to thank them individually for the roles they played. Thanks to Gretchen Pendley (for refreshing the air in times of doubt), Pat Lawless, Chris Adams, and Tracy Hawkins (for maintaining alive the laughs in the building without windows).

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I owe special thanks to the CTFS, for use of the inventory data collected from plots in the PCW, which were used not only for gradient analysis of the vegetation, but also were helpful in finding seed trees. This thesis is another contribution of the Center for understanding tropical forests.

Neighbors and friends play a very important role when you are far from your home country. I thank God for putting me in the neighborhood with José, Cecilia, Mario, Gabriela, Marquitos, Cindy, Valeria, and Virginia during my two years in Lexington. Their friendship was the exact emotional support I needed, and it came at the right moment.

Finally, and most importantly, I would like to thank my family for coming along with me. My daughters, Samantha and Nadia, left behind friends, “boyfriends”, house, school, everything in Panama, and that was so hard for the two of them. Samy and Nadia had words of encouragement for me at my weakest moments, and they also learned a lot from this experience, as anybody as brilliant as they are would have. (Your mom loves you, and wishes to be a good example of life.) Salomón, my husband, put lots of projects on hold in Panama and silenced the homesickness inside him each day to be able to give me strength to finish. Salomón cooked, washed clothes, cleaned the house, found a job, and he still had time to hug me and pace me, day-by-day, step-by-step, to the end. You are right Salo: hard times are like a rope that tightens the love between us, confirming that we can count on each other.

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# INTRODUCTION

The Panama Canal Watershed (PCW) represents a special opportunity for studies of seed dormancy in the tropics with both applied and basic research objectives. Information on seed ecology obtained for species in the PCW will increase our understanding of tropical forest dynamics, and it can be applied to the development of tropical forest management techniques.

In 1998, 54% of the PCW was forested, and 43% was pasture or shrubland (Ibáñez et al., 1999). Since the watershed supplies water for the functioning of the Canal, as well for human use in the city of Panama, in the past 25 years national and international agencies have invested millions of dollars in reforestation, restoration, and sustainable development projects that involved the use of trees (Condit et al., 2001). Interest in use of native species for these projects has been increasing in the past decade. Blakesley et al. (2002) addressed the special importance of seed information for nursery planning in restoration projects that involve the use of a large number of local species. Collection timing, seed handling procedures, germination pretreatments, and storage techniques are lacking for many tropical species (Francis, 2003). Storage also is a common problem for many tropical forest trees, since their seeds are recalcitrant or intermediate, meaning that they are sensitive to desiccation and often to low temperatures, conditions traditionally considered necessary for long-term seed storage (Vázquez-Yañez and Orozco-Segovia, 1990). There is an association between late-successional moist tropical forest trees with large, moist, non-dormant seeds and desiccation sensitivity (Dickie and Pritchard, 2002; Vázquez-Yañes et al., 2000).

Few studies have been done on processing, handling, or storage of seeds of the PCW's native species. In phenology studies in a natural forest at Barro Colorado Island (BCI), in the center of the PCW, Foster (1982) reported one peak of germination and two peaks of seed dispersal. In a community level study of seed dormancy and germination on BCI, Garwood (1983) reported that fresh seeds of 50% of 180 species were dormant, and she recognized three germination syndromes: 1) a rapid-rainy syndrome, for seeds dispersed during the early rainy season, with a majority of the species being non-dormant; 2) an intermediate-dry syndrome, for seeds dispersed during the dry season, with half of the species having an intermediate dormancy period (2-16 weeks); and 3) a delayed-rainy syndrome, for seeds

dispersed during the late rainy season, with half of the species having a delayed dormancy period (≥16 weeks).

Apart from the community study carried out by Garwood (1983), which included nursery tests, information on germination patterns in natural conditions for only a few individual species native to the PCW have been reported (Acuña and Garwood, 1987; Dalling et al., 1997; Garwood, 1986; Garwood and Lighton, 1990; Kitajima and Augspurger, 1989; Silvera et al., 2003; Sork, 1985). Most information for species that occur in the PCW comes from studies done in Costa Rica, Mexico, or Brasil (Lorenzi, 1992; Ramalho Carvalho, 1994; Salazar, 2000; Salazar and Soihet, 2001; Vázquez-Yanes and Orozco-Segovia, 1993). However, populations of widely distributed species may show significant geographical variability in germination responses among seed provenances (Vázquez-Yanes and Orozco-Segovia, 1993). Thus, there is a clear need for information on germination responses from populations of the PCW, which are the usual source for seeds in local restoration projects. Information about seed ecology and management is needed to meet the objectives of conservation and sustainable projects in the PCW.

In addition to these practical reasons for seed studies in the PCW, the watershed represents a special opportunity to understand dormancy and its role as an adaptive trait that evolved in response to environmental factors. In general, the proportion of species with dormant seeds increases with decreases in precipitation in tropical and subtropical regions (Baskin and Baskin, 1998). Lowland forests across the Panamanian isthmus are dominated by a strong climatic gradient, from an average precipitation of 3300 mm/year on the Caribbean coast to 1800 mm/year on the Pacific coast (Leigh 1990), and the length of the dry season ranges from 2 to 4 months. There are clear patterns spatial organization, deciduousness, and other leaf traits of species along this gradient (Condit et al., 2000; Pyke et al., 2001; Santiago et al., 2004).

Most publications on seed dormancy have not indicated, or even suggested, the kind of dormancy that is investigated (Baskin and Baskin, 2004). These authors proposed a classification system for seed dormancy, based on Nikolaeva (1977), that attempts to accommodate adequately the diversity of kinds of dormancy mechanisms among seeds. The proposed system includes five *classes* (physiological, morphological, morphophysiological, physical, and combinational dormancy) and a hierarchical system of *levels* and *types* within

them. Considering only the species with dormant seeds, physiological, morphological, and morphophysiological dormancy decrease from tropical evergreen to tropical deciduous forest, while physical dormancy increases (Baskin and Baskin, In press).

Two conceptual models have been proposed for the evolution of physical dormancy, one for Fabaceae (Van Staden et al., 1989) and the other for Anacardiaceae (Baskin et al., 2000). These two models interpret the evolution of the impermeable seed coat as a response to increasing aridity. Few studies have been done to determine the types of dormancy found in seeds of species growing in semiervegreen tropical forest (Baskin and Baskin 1998). The rainfall gradient along the 60 km of continuous forest at the PCW represents an excellent opportunity to test the relationship between kinds of dormancy and climatic dryness.

This study, at a regional scale, presents complete and useful information about the seed ecology of 100 tree species native to the Panama Canal watershed. For each species, it includes collection system, time of fruiting, seed mass, seed moisture content, germination, and longevity in storage. This information is used to make recommendations for nursery management for restoration projects. For the first time an attempt is made to classify (to the class level) the kind of dormancy in seeds of the PCW. I looked for a relationship between kind of dormancy and seed mass, moisture content, germination patterns, and seasonality. Further, I looked for a relationship between kind of dormancy and geographical distribution of species within the watershed based on the rainfall gradient, paying particular attention to physical dormancy. Finally, information regarding longevity during shelf storage of seeds of the species studied was used to discuss desiccation sensitivity, which is a major problem for management of tropical tree seeds (Vázquez-Yanes and Orozco-Segovia, 1993). Longevity behavior was also studied in relation to the rainfall gradient.

# METHODOLOGY

## SITE DESCRIPTION

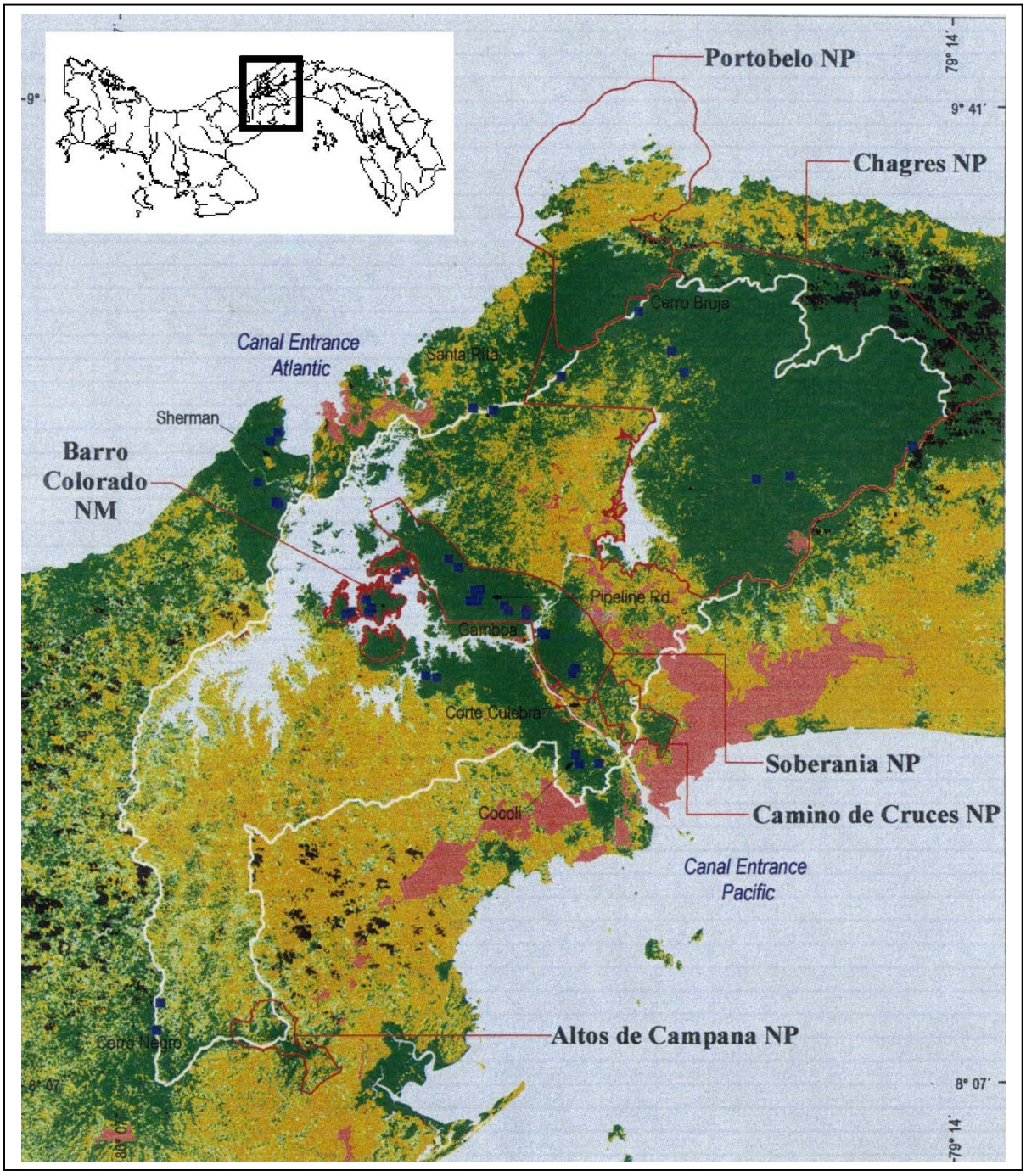
The Panama Canal, described as one as most important works of engineering in the world, was opened on August 15, 1914. This complex structural system allows the passage of ships between the Atlantic and the Pacific oceans, thus considerably reducing shipping distances between nations around the globe. Two artificial lakes were constructed to provide the water necessary to elevate ships across the isthmus topography using only gravity as the driving force. During each ship transit, approximately 52 million gallons of water are used. The total water storage capacity of the Canal is of approximately 1,660 billion gallon. However, the net capacity is approximately 365 billion gallon. Gatun Lake provides 203 billion gallon and the Alajuela Lake 162 billion gallon.

The PCW is defined as the geographic area, the surface and underground waters of which flow toward the Canal and/or are spilled into it or into its tributary lakes. The PCW encompasses 2,892 $km^2$ of land that lie at 9º north latitude in the seasonal tropics (Fig. 1). Both, temperature and humidity are relatively high throughout the year. Mean annual temperature is 27º C, with an average daily variation less than 3ºC and still less seasonal variation. Mean annual precipitation is high enough to sustain tall forest throughout the region, but there is a marked dry season from December through April (Ibáñez et al., 1999). Rainfall is higher, and the dry season shorter, on the Caribbean than on the Pacific side of the isthmus (Condit et al., 2000). Annual rainfall varies from 1,600 mm on the Pacific coast, with a 4-month dry season from December to March, to 4,000 mm north on the Caribbean coast, with a 2-3 month dry season from January to March (Condit, 1998). Most of the watershed is less than 300 m above sea level, but elevation rises to 1,000 m on three peaks to the southwest and east (Condit et al., 2001).

Most of the cities and agriculture land, mostly grassland for cattle, are located at lower elevations and on the drier Pacific side. These grasslands frequently burn during the dry season, but natural forests do not. The largest blocks of forest remain on the wetter Caribbean side of the isthmus (Condit et al., 2001).

The general structure of forests of the canal area is quite similar, except for small areas of mangrove, freshwater swamps, and mountains peaks. Large disturbances such as hurricanes

**Figure 1.** Location of Panama Canal watershed (outlined in white), based on early delimitation (The Panama Canal Authority recently expanded the official definition of the watershed). Forest is indicated in green, grass or shrubland in yellow, urban areas in pink, and water in blue. National Parks are outlined in red. Forest inventory plots are indicated with blue squares.



and fires are absent; thus, individual treefalls and small windstorms are the sole natural source of canopy turnover. A closed canopy 20-40 m tall with emergent trees reaching 50m in height and a dense understory of saplings, treelets, palms, and lianas can be found in well-drained sites (Condit et al., 2001). The majority of the watershed (90%) is classified as tropical moist forest in the Holdridge (1967) system. Small areas of wet ridges near the Atlantic are classified as wet and submontane forest, but these are not much different structurally from the moist forest (Condit, 1998).

**The remaining forests**

In 1998, only 54% of the Panama Canal watershed was forested, and 43% was pasture or shrubland (Fig. 1). Most of the forest is in two large blocks, one east of Alajuela lake and the other along the canal; the latter is usually referred as the canal corridor (Condit et al., 2001).

The Missouri Botanical Garden produced a Flora of Panama that contained an estimated 2870 species of trees and shrubs, 855 of which occurred in the Panama Canal Zone (a strip 5 km in width along both sides of the canal) (Condit et al., 2001). Pyke et al. (2001) reported 824 species of trees with a diameter at breast height ≥ 10 cm in 54 1-ha plots. Except for sites within 1-3 km of each other, no two forest are similar in terms of their dominant tree species, thus representing a regional flora with an exceptional ß-diversity (Condit et al., 2001; Pyke et al., 2001). The abrupt change in species composition is why Panama is so rich in species. Many species are extremely rare, appearing in only one of 54 1-hectare plots. However only four are endemic to Panama, and only one is restricted to the canal watershed (Condit et al., 2001).

The combination of a well-documented flora, relatively easy access to field sites, and a complex mixture of environmental gradients makes lowland Panama an excellent study area for community analysis at the landscape scale. There are clear patterns of spatial organization of species, leaf traits, and deciduous vs. evergreen life forms along this gradient (Condit et al., 2000; Condit et al., 2004; Condit et al., 2002; Pyke et al., 2001; Santiago et al., 2004). However, seed dormancy has been studied only in the Barro Colorado Island community, not at a regional level (Garwood, 1983).

## SPECIES SELECTION

We establish a preliminary list of 130 species of trees native to the PCW with ecological and/or ethnobotanic value (Aguilar and Condit, 2001). Since number of species fruiting may vary tremendously from year to year, depending on amount of seasonal rainfall and some other factors such as insect damage (Francis, 2003), the final set of species was dictated by nature (Table 1). Frequent field checks indicated the occurrence of a good fruiting season for species on the list.

*Pseudosamanea guachapele*, *Dialium guianense, Guetarda foliacea, Lafoensia punicifolia, Beilshmedia pendula,* and *Sapindus saponaria* were collected and germination assays run in 1993-1994. Methodology used for germination assays was the same except that studies on longevity, moisture content, and number of seeds per kg were not carried out in all cases. Although *Beilshmedia pendula* data include only percentage of germination and beginning and end of germination, they allow assignment of kind of dormancy.

For purposes of comparison between species, I considered the growth form and successional status reported by Condit et al. (1996b) for species on Barro Colorado Island. Growth form was defined by the authors as follows: large trees (≥20 m in height), mid-size trees (10-20 m), understory trees (4-10 m), and shrubs (1-4 m). A species was considered a gap-specialist based on demographic parameters that indicate high growth rate, high mortality, and strong tendency to recruit in gaps. Life form was reported to all 94 species for which dormancy class was assigned, and colonizing index was reported for only 34 species.

## I. SEED AND GERMINATION STUDIES

### Seed collection

Seeds were collected within the PCW and adjacent areas near the Pacific Ocean and Caribbean Sea, on both coastal sides of the Canal corridor (block of forest east and west of the Canal) (Fig. 2). Seed collection was carried out from 1996 to 1999. We made weekly field trips to select seed trees and monitor fruit set and degree of ripening. Most fruits were collected directly from the tree using a climbing system or a telescopic pole. Others fruits were collected from the ground if they were not decayed. Phenological data for individual

**Table 1.** Scientific names, synonyms, common names, and family of study species and time and area of seed collection.

| Genus | Species | Author | Common name | Family | Fruiting as reported (Months) | Month of collection | # trees collected | Collection zone |
|---|---|---|---|---|---|---|---|---|
| *Adelia* | *triloba* | (Muell.-Arg) Hemsl. | Espino amarillo | EUPHORBIACEAE | 1-4 | 5 | 1 | Center |
| *Albizia* | *adinocephala* | (Don. S.) Britton & Rose | Frijolillo | FABACEAE-MIM | | 3 | 5 | South |
| *Alseis* | *blackiana* | Hemsl. | Mameicillo | RUBIACEAE | 3,5,7-12 | 2 | 5 | Center and East |
| *Amaioua* | *corymbosa* | Kunth | Madroño de montaña | RUBIACEAE | 7-2 | 1 | 6 | Center |
| *Anacardium* | *excelsum* | (Bert. & Balb.) Skeels | Espavé | ANACARDIACEAE | 4-5- | 5 | 5 | Center and South |
| *Andira* =*Geoffroea inermis* | *inermis* | (W. Wright) Kunth | Almendro de río. Harino | FABACEAE-FAB | 8-12 | 6 | 5 | Center |
| *Annona* | *spraguei* | Saff. | Chirimoya | ANNONACEAE | 6-10 | 9 | 5 | Center |
| *Antirhea* | *trichantha* | (Griseb.) Hesml. | Candelo | RUBIACEAE | 6-10 | 8 | 5 | South |
| *Apeiba* =*A. membranacea* | *aspera* | Aubl. | Peine de Mico | TILIACEAE | 11-5 | 3 | 5 | South |
| *Apeiba* | *tibourbou* | Aubl. | Peine de mico | TILIACEAE | 1-7 | 5 | 5 | Center |
| *Aspidosperma* | *cruenta* | Woods. | Alcarreto | APOCYNACEAE | 2-5 | 10 | 5 | Center and North |
| *Beilschmiedia* | *pendula* | (Sw.) Hemsl | Agucatillo | LAURACEAE | 5-6 | 6 | 3 | Center |
| *Brosimun* | *utile* | (Kunth) Pitt. | Arbol vaca | MORACEAE | 7 | 6 | 5 | North |
| *Bursera* | *simaruba* | (L.) Sarg. | Cholo pelao | BURSERACEAE | 1-3,8 | 5 | 5 | Center and South |
| *Byrsonima* | *crassifolia* | (L.) Kunth | Nance | MALPIGHIACEAE | 5-10 | 8 | 5[1] | Center |
| *Calophyllum* | *longifolium* | Willd. | María | CLUSIACEAE | 5-12 | 9 | 5 | Center and North |
| *Calycophyllum* | *candidissimum* | (Vahl) DC. | Madroño | RUBIACEAE | 2-3 | 5 | 4 | South |
| *Carapa* =*C. nicaraguensis* | *guianensis* | Aubl. | Bateo, Tangaré | MELIACEAE | 5-8,10 | 11 | 5 | North |
| *Cassia* | *grandis* | L. f. | Caña Fístula | FABACEAE-CAES | 2-3 | 3 | 5 | North, South, East, and West |
| *Castilla* | *elastica* | Cerv. *var. costaricanum* (Liebm.) C. Berg. | Caucho | MORACEAE | 5-6 | 6 | 5 | Center and South |

Table 1. (continued)

| Genus | Species | Author | Common name | Family | Fruiting as reported (Months) | Month of collection | # trees collected | Collection zone |
|---|---|---|---|---|---|---|---|---|
| *Cedrela* | *odorata* | L. | Cedro cebolla, Cedro amargo | MELIACEAE | 1-11 | 2 | 5 | South and Campana |
| *Ceiba* | *pentandra* | (L.) Gaertn. | Ceiba | BOMBACACEAE | 1-5 | 5 | 1 | East |
| *Chrysophyllum* | *cainito* | L. | Caimito | SAPOTACEAE | 1-4 | 2 | 5 | Center, North, and South |
| *Colubrina* | *glandulosa* var. *glandulosa* | (Perkins) M.C. Johnst . | Carbonero | RHAMNACEAE | 2-4 | 4 | 5 | Center |
| *Copaifera* | *aromatica* | Dwyer | Cabimo | FABACEAE-CAES | 2-4,8-9 | 2 | 4 | South |
| *Cordia* | *alliodora* | (R. & P.) Oken | Laurel | BORAGINACEAE | 4-5 | 4 | 4 | Center |
| *Couratari* *=C. panamensis* | *guianensis* | Aubl. | Coquito | LECYTHIDACEAE | 2-3 | 2 | 1 | Center |
| *Cupania* | *latifolia* | Kunth | Gorgojero | SAPINDACEAE | 9-10 | 10 | 5 | Cerro Azul |
| *Dalbergia* | *retusa* | Hemsl. | Cocobolo | FABACEAE-FAB | 1-5,10 | 2 | 3 | Center and South |
| *Dendropanax* *=Dendropanax stenodontus* | *arboreus* | (L.) Dec. & Planch. | Muñequito | ARALIACEAE | 8-10 | 9 | 5 | Center |
| *Dialium* | *guianense* | (Aubl.) Sandwith | Tamarindo de montaña | FABACEAE-CAE | 11-3 | 3 | 1 | West |
| *Diphysa* | *robinioides* | Benth. | Macano | FABACEAE-FAB | 2-3 | 1 | 5 | South |
| *Dipteryx* *=D. panamensis* *=Oleiocarpus panamense* | *oleifera* | (Pitier) Record & Mell | Almendro de montaña | FABACEAE-FAB | 10-3 | 12 | 5 | North and West |
| *Enterolobium* | *cyclocarpum* | (Jacq.) Griseb. | Corotú | FABACEAE-MIM | 3-6 | 5 | 5 | Center and South |
| *Enterolobium* | *schomburgkii* | (Benth.)Benth | Guabino | FABACEAE-MIM | 4-9 | 4 | 5 | Center |
| *Erythrina* | *fusca* | Lour. | Palo bobo | FABACEAE-FAB | 2-5,10 | 4 | 5 | North and Center |
| *Faramea* | *occidentalis* | (L.) A. Rich. | Huesito, Jazmín | RUBIACEAE | 3-1 | 12 | 5 | Center |
| *Ficus* *=F. glabrata* | *insipida* | Willd. | Higuerón | MORACEAE | 2-4,8,10 | 7 | 5 | Center and North |
| *Genipa* | *americana* | L. | Jagua | RUBIACEAE | 1-12 | 2 | 5 | North |
| *Guarea* *=G. multiflora* | *grandifolia* | DC. | Cedro macho | MELIACEAE | 2-6,11 | 4 | 5 | Center |
| *Guarea* | *guidonia* | (L.) Sleumer | Cedro blanco. Cedro macho | MELIACEAE | 1-7,12 | 4 | 4 | Center |

Table 1. (continued)

| Genus | Species | Author | Common name | Family | Fruiting as reported (Months) | Month of collection | # trees collected | Collection zone |
|---|---|---|---|---|---|---|---|---|
| *Guazuma* | *ulmifolia* | Lam. | Guácimo | STERCULIACEAE | 3-5,9 | 3 | 5 | Center and South |
| *Guettarda* | *foliaceae* | Standl. | Guayabo de monte, espino amarillo | RUBIACEAE | 5-12 | 10 | 1 | Center |
| *Gustavia* | *superba* | (Kunth) Berg. | Membrillo | LECYTHIDACEAE | 4-8 | 7 | 8 | Center |
| *Hampea* | *appendiculata* | (Donn. Sm.) Standl. | | MALVACEAE | 1-3 | 1 | 5 | Center and North |
| *Hasseltia* *=H. guatemalensis, =H. rigida* | *floribunda* | Kunth | Parimontón | FLACOURTIACEAE | 3-6,8 | 6 | 5 | Center |
| *Heisteria* | *concinna* | Standl. | Ajicillo Naranjillo | OLACACEAE | 2-4 | 3 | 5 | Center |
| *Hura* | *crepitans* | L. | Tronador, Javillo, Ceibo | EUPHORBIACEAE | 2-4 | 2 | 5 | Center, South and East |
| *Hyeronima* *=H. laxiflora* | *alcheorneoides* | Allemao | Zapatero, Pilón, Piedro | EUPHORBIACEAE | 3-8,11 | 12 | 5 | Center |
| *Hymenaea* | *courbaril* | L. | Algarrobo | FABACEAE-CAES | 11-12,2,8 | 1 | 5 | Center and South |
| *Inga* | *punctata* | Willd. | Guabita cansaboca | FABACEAE-MIM | 3-5 | 6 | 2 | Center |
| *Inga* | *spectabilis* | (Vahl) Willd. *var. spectabilis* | Guaba machete | FABACEAE-MIM | 2-5 | 4 | 4 | Center and East |
| *Jacaranda* | *copaia* | (Aubl.) D. Don. | Jacaranda | BIGNONIACEAE | 7-8,10,1 | 9 | 5 | Center |
| *Lacmellea* | *panamensis* | (Woods.) Markgr. | Lagarto negro | APOCYNACEAE | 1-7 | 3 | 2 | Center and North |
| *Lafoensia* | *punicifolia* | D.C. | Roble coral, Cascarillo | LYTHRACEAE | 1-4 | 4 | 1 | Center |
| *Lindackeria* | *laurina* | C. Presl. | Chiriquí | FLACOURTIACEAE | 9-2 | 2 | 4 | Center and North |
| *Lonchocarpus* *=L. pentaphyllus* | *latifolius* | Kunth | Zorro, Gallote | FABACEAE-FAB | 3-5 | 9 | 2 | Center and North |
| *Luehea* | *seemannii* | Triana & Planch | Guácimo colorado | TILIACEAE | 4-5,8 | 6 | 5 | Center and South |
| *Luehea* | *speciosa* | Willd. | Guácimo pacheca | TILIACEAE | 4-6 | 2 | 30 | West |
| *Margaritaria* | *nobilis* | L. f. | Clavito | EUPHORBIACEAE | 7-10 | 10 | 5 | Center |
| *Miconia* *=M. astroplocama* | *argentea* | (Sw.) DC. | Papelillo, Dos caras | MELASTOMATACEAE | 1-6 | 4 | 5 | Center |

Table 1. (continued)

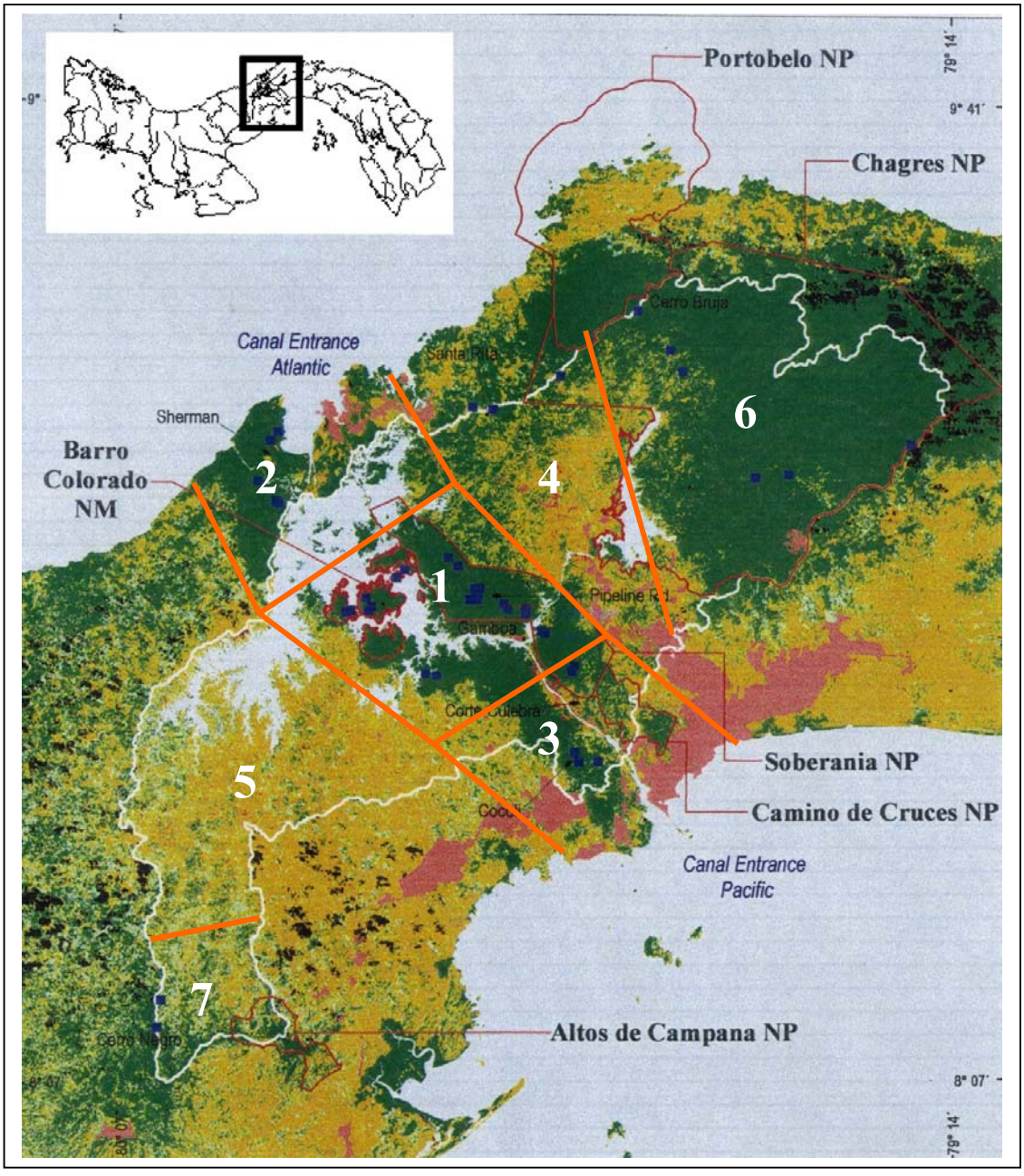
| Genus | Species | Author | Common name | Family | Fruiting as reported (Months) | Month of collection | # trees collected | Collection zone |
|---|---|---|---|---|---|---|---|---|
| *Miconia* =*M. borealis* | *minutiflora* | (Bonpl.) DC. | Dos caras | MELASTOMATACEAE | 2-3 | 4 | 5 | Center |
| *Ochroma* | *pyramidale* | (Lam.) Urb. | Balso | BOMBACACEAE | 1-3,5-8 | 2 | 5 | Center, North,and South. |
| *Ormosia* | *macrocalyx* | Ducke | Conejito colorao | FABACEAE-FAB | 3-11 | 8 | 5 | South |
| *Pachira* =*Pochota quinata,* =*Bombacopsis quinata* | *quinata* | (Jacq.) W.S. Alverson | Cedro Espino | BOMBACACEAE | 1-6 | 3 | 5 | Center |
| *Phoebe* =*P. mexicana* =*P. costaricana* | *cinnamomifolia* | (Kunth) Kiesterm, | Sigua blanco | LAURACEAE | 4-8 | 8 | 5 | Center Campana |
| *Platymiscium* =P. polystachyum | *pinnatum* | (Jacq.) Dugand | Quira | FABACEAE-FAB | 8-3 | 1 | 5 | West |
| *Posoqueria* | *latifolia* | (Rudge) Roem. & Schult. | Boca de vieja | RUBIACEAE | 1-12 | 12 | 5 | Center and South |
| *Prioria* | *copaifera* | Griseb | Cativo | FABACEAE-CAES | 3-6,10 | 7 | 5 | Center |
| *Protium* | *panamense* | (Rose) J. M. Johnst. | Chutrás | BURSERACEAE | 9-11,2-6 | 12 | 3 | North |
| *Protium* | *tenuifolium* | Engl. | Chutrás | BURSERACEAE | 9-10 | 9 | 5 | Center |
| *Pseudobombax* | *septenatum* | (Jacq.) Dugand | Barrigón | BOMBACACEAE | 2-4 | 4 | 5 | Center and South |
| *Pseudosamanea* =*Albizia guachapele* | *guachapele* | (Kunth) Harms | Guachapalí | FABACEAE-MIM | 10-3 | 11 | 3 | South |
| *Pterocarpus* =*P. hayesii* | *rohrii* | Vahl | Sangre de gallo | FABACEAE-FAB | 8-11 | 8 | 3 | Center |
| *Quararibea* | *asterolepis* | Pittier | Guayabillo | BOMBACACEAE | 8-11,1,5 | 9 | 5 | Center |
| *Sapindus* | *saponaria* | L. | Jaboncillo | SAPINDACEAE | 11-5 | 3 | 1 | South |
| *Sapium* =*S. biglandolosum* =*S. aucuparium* | *glandulosum* | (L.) Morong | Olivo | EUPHORBIACEAE | 5-10 | 9 | 5 | Center |
| *Schefflera* =*Didymopanax morototoni* | *morototoni* | (Aubl.) Maguirre, Stey., & Frod. | Guarumo de Pava | ARALIACEAE | 1-12 | 2 | 5 | Center and South |
| *Spondias* | *mombin* | L. | Jobo | ANACARDIACEAE | 7-9 | 8 | 5 | South and North |
| *Spondias* | *radlkoferi* | Donn. Sm. | Jobo | ANACARDIACEAE | 9-12 | 10 | 5 | Center |

Table 1. (continued)

| Genus | Species | Author | Common name | Family | Fruiting as reported (Months) | Month of collection | # trees collected | Collection zone |
|---|---|---|---|---|---|---|---|---|
| *Sterculia* | *apetala* | (Jacq.) Karst. | Panamá | STERCULIACEAE | 1-3 | 2 | 5 | South |
| *Swietenia* | *macrophylla* | King | Caoba | MELIACEAE | 1-4,8 | 1 | 5 | Center and South |
| *Tabebuia* | *guayacan* | (Seem.) Hemsl. | Guayacán | BIGNONIACEAE | 3-6 | 5 | 4 | South |
| *Tabebuia* | *rosea* | (Bertol) DC. | Roble | BIGNONIACEAE | 3-5 | 4 | 5 | South |
| *Tachigalia* | *versicolor* | Standl. & L.O. Wms. | Arbol suicida | FABACEAE-CAES | 8-3 | 2 | 5 | Center and North |
| *Tapirira* | *guianensis* | Aubl. | Palo de gusano | ANACARDIACEAE | | 9 | 7 | North |
| *Terminalia* | *amazonia* | (J.F. Gmel.) Exell | Amarillo | COMBRETACEAE | 2-6 | 4 | 5 | Center and South |
| *Trattinnickia* | *aspera* | (Standl.) Swart | Caraño hediondo | BURSERACEAE | 2-4,10-12 | 10 | 1 | Center and North |
| *Trema* | *micrantha* | (L.) Blume | Jordancillo<br>Capulín macho | ULMACEAE | 6-10 | 8 | 5 | Center, South, and Campana |
| *Trichilia* | *hirta* | L. | Matapiojo | MELIACEAE | | 3 | 5 | Center and South |
| *Trichilia*<br>*=T. cipo* | *tuberculata* | (Trina & Pllanch) C. DC. | Alfajía Colorado | MELIACEAE | 5-8,10-11 | 9 | 6 | Center |
| *Trichospermum*<br>*=T. mexicanum belotia* | *galeottii* | (Turcz.) Kosterm. | Burrilico | TILIACEAE | 2-4 | 1 | 5 | Center |
| *Triplaris* | *cumingiana* | Fischer & Meyer | Palo Santo | POLYGONACEAE | 3-5 | 4 | 5 | Center |
| *Vantanea*<br>*=V. occidentalis* sensu Flora of Panama | *depleta* | McPherson | Chiricano | HUMIRIACEAE | 2 | 2 | 3 | Center |
| *Virola* | *sebifera* | Aubl. | Velario | MYRISTICACEAE | 7-2 | 9 | 4 | North |
| *Virola*<br>=V. nobilis | *surinamensis* | (Rol.) Ward | Velario | MYRISTICEAE | 2-8,10 | 5 | 5 | Center and North |
| *Vochysia* | *ferruginea* | Mart. | Mayo | VOCHYSIACEAE | 6-9 | 10 | 5 | Center and North |
| *Xylopia* | *aromatica* | (Lam.) Mart. | Malagueto hembra | ANNONACEAE | | 12 | 5 | Center and South |
| *Xylopia* | *frutescens* | Aubl. | Malagueto macho | ANNONACEAE | 11-2 | 1 | 5 | Center |
| *Zanthoxylum* | *panamense* | P. Wilson | Arcabú | RUTACEAE | 8-12 | 12 | 5 | Center |

Fruiting as reported by Croat (1978), Foster (1982), and Wright (personnal communication). Definitions of collection zones are given in Fig. 2.

**Figure 2.** Collection zones of tree seeds defined based on rainfall, topography, and human disturbance. 1, Center (lowland forest, intermediate rainfall, low disturbance); 2, North (lowland forest, high rainfall, low disturbance); 3, South (lowland forest, low rainfall, intermediate-high disturbance); 4, East (lowland forest, intermediate rainfall, high disturbance); 5, West (lowland forest, high disturbance, intermediate rainfall); 6, Chagres National Park (submontane forest, low disturbance, high rainfall); 7, Campana National Park (submontane forest, intermediate disturbance, intermediate rainfall).



tree species on nearby Barro Colorado Island (Croat, 1978; Foster, 1982) were used in organizing the collection effort. Collection and processing problems are species-driven, and many poorly known species in the tropics represent a challenge to handle (Francis, 2003). Thus, in each case trees were identified by number, location recorded, and fruit/seed collecting and cleaning methods used. Seeds were separated from the fruits and mixed.

For most species, fruits were collected from at least five healthy individuals that had fruits ripening at the same time. Seeds were collected from only one tree each of *Adelia triloba*, *Ceiba petandra*, and *Trattinnicki aspera*; from only two trees of *Inga punctata* and *Lonchocarpus latifolius*; from three trees of *Dalbergia retusa*, *Pterocarpus rorhii,* and *Vantanea depleta*; and from four trees of *Calycophyllum candidisimun*, *Copaifera aromatica*, *Guarea guidonea*, *Inga spectabilis*; *Tabebuia guayacan*, and *Virola sebifera* (Table 1). Seeds of *Luehea speciosa* were collected from 30 individuals due to scarce fruit production.

**Number of seed per kg / seed weight**

Following the recommended protocols of the International Seed testing Association rules (ISTA, 1993), eight groups of 100 seeds were weighed and averaged to calculate the number of seeds per kilogram, after mixing seeds from parent trees. The number was also expressed as seed weight for comparisons. I delimited six categories for seed size based on seed weight following Foster (1982) and included within these categories four of the species without seed weight data based oin seed information from the literature. Salazar (2000) reported seed weight for *Dipteryx panamensis,* and Pearson et al. (2002) reported it for *Alseis blackiana.* The seed weight category (1-10g) for *Beilschmiedia pendula* and *Guettarda foliacea* was inferred from seed size and fruit type (drupes).

**Moisture content (ISTA rules)**

Moisture content for freshly collected diaspores was calculated immediately after cleaning process following recommended protocols of the International Seed testing Association rules (ISTA, 1993). Two replicates of 4 to5 g were weighed, dried for 17 h at

103 ˚C, and then reweighed. Seeds larger than 1cm were cut into smaller pieces for drying. Both diaspores (samaras) and seeds were evaluated for *Platymiscium pinnatum*. Moisture content of *Trattinnickia aspera* corresponds to seeds collected for the first time, which did not germinate at all, and germination data are for seeds from a second collection whose moisture content was not evaluated. *Tachigalia versicolor* moisture content is for the samaras (diaspores) of the five trees collected, and germination data are for seeds from only two trees, since those from the other three trees appeared not to be viable. Thus, moisture content does not correspond to the unit evaluated in germination.

**Germination tests**

Fruits collected from all trees were cleaned, and the dispersal units (diaspore) were mixed and sown immediately after cleaning process finished (within the 1-7 days). Throughout this thesis, "seed" means a true seed or a diaspore. Species whose diaspores included endocarps of drupes were: *Anacardium excelsum, Andira inermis, Beilschmiedia pendula, Dipteryx oleifera, Spondias mombin,* and *S. raldkoferii*. Only diaspores of *Spondias* spp. were multiseeded. Although multiple germination occurred in the two *Spondias* spp., it was not very frequent; thus, the count was done only once per diaspore (i.e. counted as one).

Four replicates of 100 seeds were sown on oven-sterilized sand in plastic trays. Large seeds were pushed into the sand for one-half of their thickness. Small seeds were covered by 3-5 mm of sand, but after watering most of them became partially uncovered. Thus, they were exposed to light. However, due to shortage of seeds for *Calophyllum longifolium, Lonchocarpus latrifolius, Luehea speciosa, Dipteryx oleifera*, and *Gustavia superba,* we sowed five replicates of 25 seeds, and for *Hymenaea courbaril* we sowed four replicates of 50 seeds. Two species, *Carapa guianense* and *Prioria copaifera*, had large seeds that did not fit into the trays; thus, we sowed four replicates of 50 seeds directly in pots. Conditions in the nursery were similar to those in commercial production nurseries in Panama (ambient temperature (25-31ºC, 30% full sunlight, watered twice daily with an automated sprinkler system). The studies were done without any seed pretreatment to learn about natural dormancy. Exceptions were the removal of the aril from *Sapium glandulosum, Virola*

*surinamensis, V. sebifera*, and *Lindackeria laurina* and cutting the wing in *Swietenia macrophylla, Pterocarpus rorhii,* and *Aspidosperma cruenta,* to avoid fungal growth and economize space.

Germination, defined as radicle emergence, was monitored weekly until four weeks without germination (after a clear peak occurred) to a maximum of 10 months. *Enterolobium cyclocarpum, E. schomburgkii*, and *Faramea occidentalis* were monitored for 11 months. Total germination, standard deviation of total germination, and coefficient of variation of total germination between replicates were calculated. Median (MLG) and mean (MeanLG) length of germination period for all seeds that germinated were calculated as measures of dormancy. Standard deviation of mean germination time (STD MLG) and total germination time (STD Germ) (time until the last seed germinated) were calculated.

In some cases where germination percentages were low and number of seeds collected sufficient, we tested pretreatments to break dormancy, using mechanical scarification for *Colubrina glandulosa* (Ramalho Carvalho, 1994), *Pseudosamanea guachapele*, *Enterolobium cyclocarpum,* and *E. schkomburgkii* (Salazar, 2000), *Cassia grandis*, and *Sapindus saponaria*; submergence during two minutes in warm water (80ºC) for *Apeiba aspera*, *Luehea seemannii*, and *A. tibourbou* (Acuña and Garwood, 1987), then allowing them to cool to room temperature before sowing; and the latter treatment followed by 24 hours in running tap water for *Guazuma ulmifolia* (Salazar, 2000).

**Longevity studies**

Seeds were stored in paper bags at 20˚C and 60% relative humidity. Storage conditions were chosen considering the best conditions in many local field projects, where cold rooms are not available. Since many seeds had high moisture content, paper bags were preferred to plastic ones to avoid fungal growth. Fungicide (Vitavax) was applied to *Copaifera aromatica*, *Trema micrantha,* and *Virola surinamensis*. For each species with enough seed collected, five replicates of 20 seeds were sown each month in the same nursery conditions described above, and germination was monitored until it has decreased to <5%, or until the seeds in the lot were used up.

I considered seeds with a viability period of 1 month or less to be very short-lived, those with a viability period between 1 and 4 months short-lived, and those with a viability period

more than 4 months long-lived. Species whose final germination percentage was > 5% before the 4-months of storage, but longevity studies were not continued due to lack of seeds, were considered to be long-lived, and species with initial total germination < 10% were not considered for longevity categories. *Carapa guianensis* and *Cordia alliodora* were assigned to very short and long-lived categories, respectively, based on reports in the literature (Salazar, 2000, Tweddle et al., 2003a).

**Nursery management constraints**

Following Blakesley et al (2002), we calculated the month of peak of germination for each species, taking into consideration month of collection and median length of germination period. For example, seeds collected in November with a MLG of 62 days will have a peak of germination in January. Then, I graphed the number of species that had their peak of germination for each month. Both field work needed for collection and nursery work have been analyzed to predict nursery management constraints.

## II. ASSIGNMENT TO SEED DORMANCY CLASS

For the purpose of this thesis, a seed is considered dormant if the median length of germination time without any treatment is 30 days or longer. I grouped species into those with non-dormant and dormant seeds. Further, following Baskin and Baskin (2004) I made subgroups with five different classes of dormancy: 1) physical dormancy, species with a water impermeable seed coat; 2) morphological dormancy, species with an underdeveloped embryo and MLG≤30 days; 3) morphophysiological dormancy, those with an undeveloped embryo and MLG>30 days; 4) physiological dormancy, those that have a permeable seed coat and a fully-developed embryo; and 5) combinational dormancy (physical + physiological), species with an impermeable seed coat and a physiologically dormant embryo.

A seed was consider to have physical dormancy if it did not imbibe water and/or when the species belongs to a family, or to one of its taxonomic subdivisions (e.g., Anacardiaceae, *Rhus* complex) known to have physical dormancy (Baskin et al., 2000). For the imbibition test, I followed the method described by Bansal et al. (1980). The diaspores (dispersal units)

were weighed and placed on moist filter paper at room temperature (ca. 22º C). Then, at time 0 and at hourly (or shorter) intervals for 8-24 hr seeds were removed from the wet paper, blotted dry, and reweighed. Percentage water uptake was calculated as actual increase in seed mass based on seed mass at time 0:

$$\%W_s = [(W_i - W_0)/W_0] \times 100,$$

where $\%W_s$= percentage increase in seed weight, $W_i$= weight after a given interval of time i, and $W_0$= seed weight at time 0. An increase in seed weight indicates that seeds (or fruits) have water-permeable coats, whereas no increase in weight indicates that they have water-impermeable coats. When possible, water uptake was compared in scarified seeds vs. non-scarified seeds (hot- water or mechanical scarification). Mechanical scarification (with a file or knife) was applied to seeds for which their size and shape allowed for this treatment to be administered.

A seed was considered to have morphological or morphophysiological dormancy if it had an underdeveloped embryo (determined by conducting microscopic examination of the seeds, if available) and/or belongs to a family known to have an underdeveloped embryo, as listed in Baskin & Baskin (1998). A seeds was considered to have morphophysiological dormancy if it had an underdeveloped embryo and an MLG> 30 days.

## III. ANALYSIS OF SEED DORMANCY AND SEED STORAGE BEAHAVIOR ALONG THE RAINFALL GRADIENT

The Center for Tropical Forest Science (CTFS) has established a series of 1-ha inventory plots along the nearly continuous corridor of tall, closed-canopy forest that flanks the Panama Canal. The main purpose of these plots is for floristic and forest dynamic studies. I compared the proportion of species with each class of dormancy (sensu Baskin and Baskin 2004) along the gradient based on inventory data from the CTFS for 39 of these permanent plots. Average annual rainfall in the plots ranges from 1887 to 3072 mm (Condit et al., 2004). I divided the entire range into five regions of equal-range units of mean annual precipitation: 1887-2124 mm, 2125-2360 mm, 2361-2598 mm, 2599-2835 mm, and 2836-3072 mm. Each of the five regions, defined based on equal increments within the total range of precipitation these 39 plots cover, included different numbers of plots. Since I considered all information available valuable to describe forest composition, I did not discard any of it, and thus, zones are

represented by different numbers of plots: zone 1 (1887-2124 mm) includes CTFS plots # C1-C4, P29, and P30; zone 2 (2125-2360 mm) plots P23 - P28; zone 3 (2361-2598 mm) plots P05-P08, P10, P12 -P17, P21, and P22; zone 4 (2599-2835) plots P11 and P18 - P20; and zone 5 (2836-3072 mm) plots P01 - P04, P09, and S0 to S4.

Presence of my study species in any of the plots for each of the five regions was tabulated. The proportion of species with each class of dormancy for each rainfall category was calculated, based on total species and on those with dormant seeds. These data were graphed to determine if there was any trend of dormancy class vs. rainfall gradient. Similar tabulations and graphs were done to determine if there was any trend of longevity categories vs. rainfall gradient. For the purposes of comparison, I combined short-lived + very short-lived categories.

**IV. STATISTICAL ANALYSES**

Comparisons between sowing pretreatments were done using one-way analysis of variance (ANOVA) of final germination percentages in each treatment. Linear model regressions were conducted for *Spondias mombin* to establish the relationship, if any, between total germination and time of storage.

Box plots showing median, quartiles, outliers, and extremes were generated to explore relationships between month of collection, MLG, kind of dormancy, seed size, dispersal time, longevity, and MC, after establishing categories of the latter four variables. Differences between these categories were tested using the Tukey HSD test. A scatter plot was generated to explore the relationship between MC and seed weight.

Pearson correlation coefficients were calculated between all variables for germination studies, and to establish the relationship between precipitation gradient and both proportion of dormancy classes and longevity categories

All statistical tests were carried on with Statistical software SPSS® Base 12 (2003).

# RESULTS

## I. SEED AND GERMINATION STUDIES

### Seed collection

The best method for collecting seeds was to use a telescopic pole, which allowed access to the crown of 88 (of 100) species of trees less than 20 m tall. Enough seeds of only eight species were collected from the ground, and for 23 species both methods were needed. For 18 species, the trees had to be climbed to complete seed collection, six of which were only accessible by climbing (Table 2). Unfortunately, seeds of *Platymiscium pinnatum* and *Couratari guianens,* two species that required climbing to collect, did not germinate at all, probably due to inviability caused by insect attack.

Seeds were collected from a total of 100 species, and for 94 of these I obtained results for which I am confident to discuss dormancy. The species from which seeds were collected belong to 34 families. Families represented by the most species are Fabaceae (21, including the three subfamilies), Rubiaceae (8), Meliaceae (7), Tiliaceae (5), Bombacaceae (5), and Anacardiaceae (4) (Fig. 3).

In many species, exact timing of fruit maturation was unknown, and approximately 20% of those with fruiting phenology records were collected in a season different from that in which the fruits were reported to ripen (Table 1). In agreement with data for canopy and understory trees from BCI (Foster, 1982), I found two peaks of fruiting: January-June and August-October. Only four species were collected in July, two in December, and one in November (Fig. 4).

**Table 2.** Method of collection and of cleaning seeds of 100 native species from the Panama Canal Watershed.

| Species | Collection method | Fruit/seed cleaning method |
|---|---|---|
| *Adelia triloba* | From tree with pole | Capsules opened into paper bags, seed extracted manually |
| *Albizia adinocephala* | From tree with pole and from ground | Break capsules manually. |
| *Alseis blackiana* | From tree with pole | Break capsules manually. |
| *Amaioua corymbosa* | From tree with pole | Break capsules manually. |
| *Anacardium excelsum* | From ground | Fruit = diaspore, does not need cleaning |
| *Andira inermis* | From tree with pole | Extract exocarp with knife. |
| *Annona spraguei* | From tree with pole | Separate seeds from fleshy fruit wall under water. |
| *Antirhea trichantha* | From tree with pole | Separate seeds from fleshy fruit wall under water. |
| *Apeiba aspera* | From ground | Break capsules manually. |
| *Apeiba tibourbou* | From tree with pole | Break capsules manually. |
| *Aspidosperma cruenta* | From tree, climbing | Break capsules manually. |
| *Beilschmedia pendula* | From tree with pole | Separate seeds from fleshy fruit wall manually. |
| *Brosimun utile* | From tree, climbing | Separate seeds from fleshy fruit wall manually. |
| *Bursera simaruba* | From tree with pole | Break capsules manually. |
| *Byrsonima crassifolia* | From tree with pole | Separate seeds from fleshy exocarp manually. |
| *Calophyllum longifolium* | From tree, climbing | Separate seeds from fleshy fruit wall manually. Seeds germinated in bag. |
| *Calycophyllum candidissimum* | From tree with pole and with sheets | Winged seeds are collected in sheets and do not need cleaning. |
| *Carapa guianensis* | From tree, climbing | Capsule opens alone. |
| *Cassia grandis* | From tree with pole | Break the legume manually. |
| *Castilla elastica* | From tree with pole and from ground | Separate seeds from fleshy fruit wall under water. |
| *Cedrela odorata* | From tree with pole | Let capsules open in dry area, and extract winged seeds manually. |
| *Ceiba pentandra* | From tree with pole and from ground | Let capsules open in dry area, and separate kapok (fibers around the seeds) manually. |
| *Chrysophyllum cainito* | From tree, climbing | Separate seeds from fleshy fruit wall under water, or eat it. |
| *Colubrina glandulosa* | From tree with pole and with sheets | Let capsules open in dry area, and extract seeds manually. |
| *Copaifera aromatica* | From tree with pole and from ground | Extract aril manually. |
| *Cordia alliodora* | From tree with pole | Break capsules manually, and extract seeds manually. |
| *Couratari guianensis =C. panamensis* | From tree, climbing | Let capsules open in dry area, and extract seeds manually. |
| *Cupania latifolia* | From tree with pole | Let capsules open in dry area. Extract seeds manually, and extract aril. |
| *Dalbergia retusa* | From tree with pole | Break legume manually. |
| *Dendropanax arboreus* | From tree with pole | Separate seeds from fleshy fruit wall manually. |
| *Diphysa robinioides* | From tree with pole | Break legume manually. |
| *Dipteryx oleifera =D. panamensis* | From ground | Fruit = disapore, does not need cleaning |
| *Enterolobium cyclocarpum* | From ground | Break legume manually (easier in a bag), separate seeds, and wash them to extract sweet mesocarp. |
| *Enterolobium schomburgkii* | From ground | Break legume manually (easier in a bag), and separate seeds, and wash them to extract sweet mesocarp. |
| *Erythrina fusca* | From tree with pole | Break legume manually. |

**Table 2.** (continued)

| Species | Collection method | Fruit/seed cleaning method |
|---|---|---|
| *Faramea occidentalis* | From ground | Separate seeds from fleshy fruit wall under water. |
| *Ficus insipida* | From tree with pole and climbing | Let the fleshy fruit dry, and extract seeds manually. Probably flotation method could be useful to distinguish empty fruits (discharge the ones that float). |
| *Genipa americana* | From tree with pole | Separate seeds from fleshy fruit wall under water. |
| *Guarea grandifolia* | From tree with pole | Let capsules open in dry area. |
| *Guarea guidonia* | From tree with pole | Let capsules open in dry area. |
| *Guazuma ulmifolia* | From tree with pole and from ground | Break fruit and extract seeds manually. |
| *Gustavia superba* | From tree with pole and from ground | Open fruits carefully with a knife to extract seeds. |
| *Hampea appendiculata* | From tree with pole | Let capsules open in dry area. Extract aril. |
| *Hasseltia floribunda* | From tree with pole | Separate seeds from fleshy fruit wall manually. Select black fruits. |
| *Heisteria concinna* | From tree with pole and climbing | Remove tiny fleshy exocarp. Endocarp is part of the diaspore. |
| *Hura crepitans* | From tree with pole | Put capsules in a cloth bag, then hit them or let them fall, so they will explode, liberating the seeds. |
| *Hyeronima alcheorneoides* | From tree, climbing | Fruit = disapore, does not need cleaning |
| *Hymenaea courbaril* | From tree with poles, climbing, and from ground | Break fruit and extract seeds manually. A hammer is needed to break the indehiscent fruit. |
| *Inga punctata* | From tree with pole and from ground | Break fruit and extract seeds manually. Extract sweet aril by hand, or better eat it! |
| *Inga spectabilis* | From tree with pole | Break fruit and extract seeds manually. Extract sweet aril by hand, or better eat it! |
| *Jacaranda copaia* | From tree climbing | Let capsules open in dry area. |
| *Lacmellea panamensis* | From ground | Separate seeds from fleshy exocarp manually. Seeds germinated in the bag. |
| *Lindackeria laurina* | From tree with pole | Let capsules open in dry area. |
| *Lonchocarpus latifolius* | From tree with pole | Break capsules manually. |
| *Luehea seemannii* | From tree with pole | Let capsules open in dry area. |
| *Luehea speciosa* | From tree with pole | Let capsules open in dry area. |
| *Margaritaria nobilis* | From tree with pole | Let capsules open in dry area. |
| *Miconia argentea* | From tree with pole | Separate seeds from fleshy fruit wall under water. Collect the tiny seeds in cheesecloth. |
| *Miconia minutiflora* | From tree with pole | Separate seeds from fleshy fruit wall under water. Collect the tiny seeds in cheesecloth. |
| *Ochroma pyramidale* | From tree with pole. | Break capsules manually. Separate hairs from the seed using a sieve. |
| *Ormosia macrocalyx* | From tree with pole and from ground. | Let capsules open in dry area. |
| *Phoebe cinnamomifolia* | From tree with pole and from ground | Separate seeds from fleshy fruit wall under water and wash. |
| *Platymiscium pinnatum* | From tree, climbing | We extracted seeds from the samaras, but are not completely confident about their maturity. |
| *Pochota quinata* | From tree with pole | Let capsules open in dry area. |
| *Posoqueria latifolia* | From tree with pole | Separate seeds from fleshy fruit wall under water. |
| *Prioria copaifera* | From ground | Seeds are collected clean. |

**Table 2.** (continued)

| Species | Collection method | Fruit/seed cleaning method |
|---|---|---|
| *Protium panamense* | From tree with pole | Break capsules manually. Eliminate aril. |
| *Protium tenuifolium* | From tree with pole | Break capsules manually. Eliminate aril. |
| *Pseudobombax septenatum* | From tree with pole | Let capsules open in dry area. Separate hairs from seeds using a sieve. |
| *Pterocarpus rohrii* | From tree climbing | Cut wing. |
| *Quararibea asterolepis* | From ground | Separate seeds from fleshy fruit wall, and let seeds air-dry. |
| *Sapium glandulosum* | From tree with pole and climbing | Let capsules open in dry area, and extract aril manually under water. |
| *Schefflera morototoni* | From tree with pole and from ground | Separate seeds from fleshy fruit wall under water. |
| *Spondias mombin* | From tree with pole and from ground | Remove fleshy exocarp under water. Endocarp is part of diaspore. |
| *Spondias radlkoferi* | From tree with pole and from ground | Remove fleshy exocarp under water after making several cuts. Endocarp is part of diapore. |
| *Sterculia apetala* | From tree with pole and from ground | Let capsules open in dry area. Extract seeds manually being very careful with the hairs in the fruit wall. |
| *Swietenia macrophylla* | From tree with pole and climbing | Let capsules open in dry area. Cut wing. |
| *Tabebuia guayacan* | From tree with pole | Let capsules open in dry area. Cover them to avoid seed loss by wind. |
| *Tabebuia rosea* | From tree with pole | Let capsules open in dry area. Cover them to avoid seed loss by wind. |
| *Tachigalia versicolor* | From ground | Fruit = diaspore, does not need cleaning. Mature fruit can be recognized by the rastled-sound the dry seeds make inside when fruit is shaken. Also, seeds can be extracted from samaras and sown. |
| *Tapirira guianensis* | From tree with pole | Break fruit and extract seeds manually.. |
| *Terminalia amazonia* | From tree with pole and from ground | Fruit = diaspore, does not need cleaning. However, it is very difficult to distinguish empty fruits from filled ones. |
| *Trattinnickia aspera* | From tree with pole | Separate seeds from fleshy fruit wall manually. |
| *Trema micrantha* | From tree with pole | Dry Fruit = diaspore, does not need cleaning. |
| *Trichilia hirta* | From tree with pole | Let capsules open in dry area. |
| *Trichilia tuberculata* | From tree with pole | Let capsules open in dry area. |
| *Trichospermum galeottii* | From tree with pole | Let capsules open in dry area. |
| *Triplaris cumingiana* | From tree with pole | Fruit = diaspore, does not need cleaning, We cut wings. |
| *Vantanea depleta* | From tree with pole | Separate seeds from flesh exocarp manually with a knife. |
| *Virola sebifera* | From tree with pole | Let capsules open in dry area. |
| *Virola surinamensis* | From tree with pole | Let capsules open in dry area. |
| *Vochysia ferruginea* | From tree with pole | Let capsules open in dry area. |
| *Xylopia aromatica* | From tree with pole | Let capsules open in a plastic bag. |
| *Xylopia frutescens* | From tree with pole | Let capsules open in a plastic bag. |
| *Zanthoxylum panamense* | From tree with pole | Let capsules open in dry area. |

**Figure 3.** Number of species studied in each of the 34 families. Fabaceae has been subdivided into its three subfamilies.

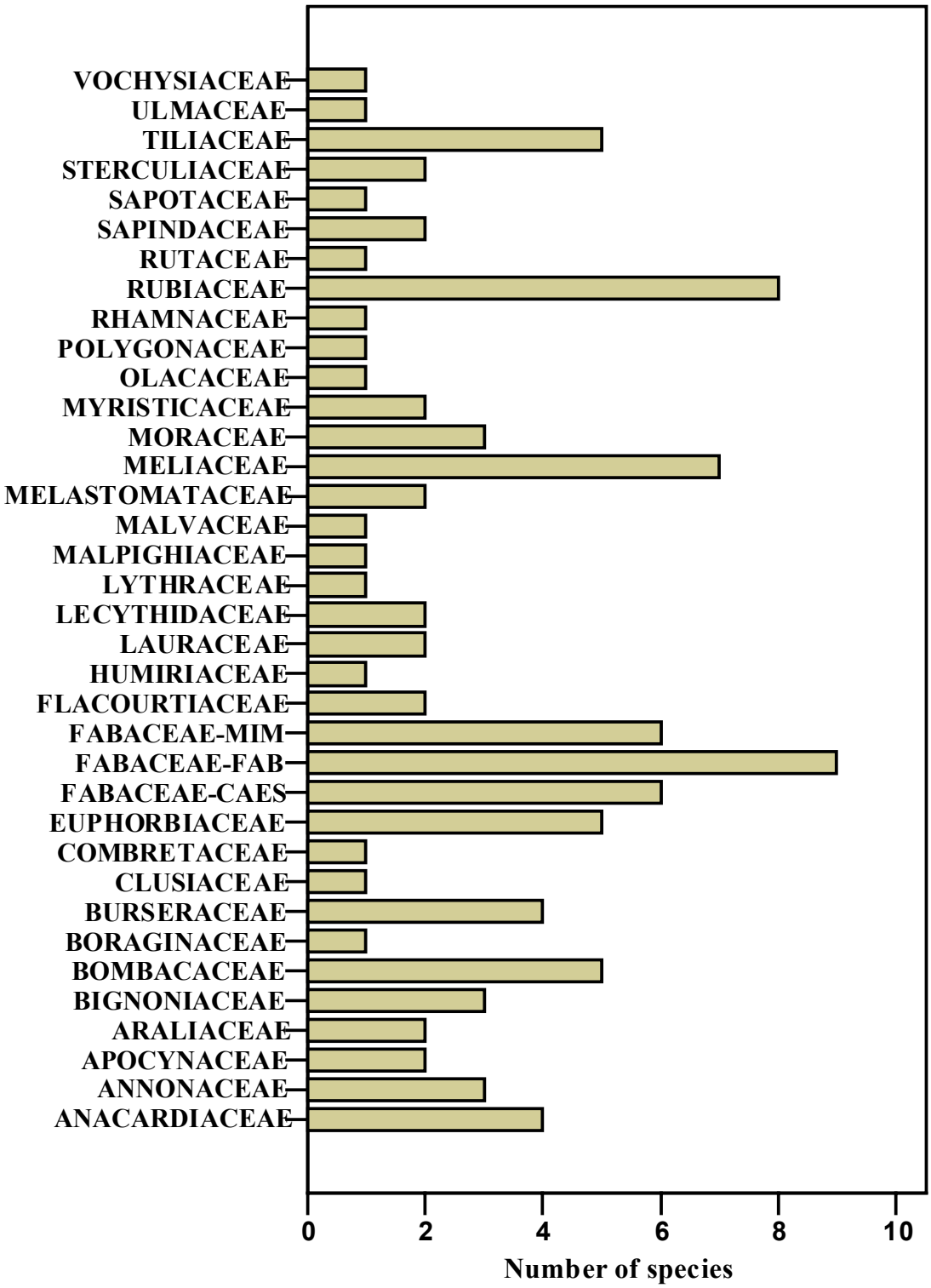
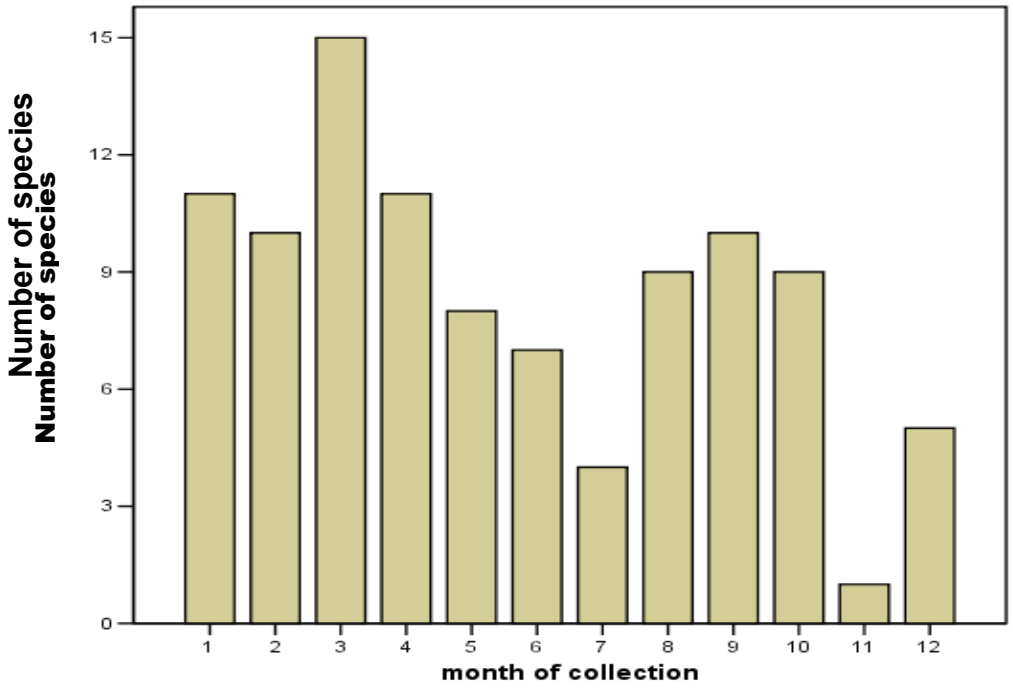


**Figure 4.** Number of species whose seeds were collected in each month.




**Number of seed per kilogram / seed weight**

Number of seeds per kilogram was obtained for 95 of the study 100 species (Table 3). The number ranged from 17 to 11,682,243. Expressed as seed weight, the frequency distribution is remarkably right skewed (skewness 6.21) and peaked (kurtosis 39.69), with a mean of 1.96 g and a median of 0.13 g (Table 4). I grouped 99 of the species into seed weight categories: five species (5.1%) had seeds that weighed less than 0.001g (>1,000,000 seed/kg); 12 (12.1%) 0.001 to 0.01g (1,000,000-100,000 seed/kg); 30 (30.3%) 0.01 to 0.1g (100,000-10,000 seeds/kg); 32 (32.3%) 0.1 to 1 g (10,000-1,000 seeds/kg); 16 (16.2%) 1 to10 g (100-1,000 seeds/kg); and four (4 %) >10 g, (<100 seeds/kg) (Fig. 5).

**Table 3.** Results of germination and other studies of 100 species native to the Panama Canal Watershed. Seeds/kg: number of seeds (or diaspore)/kg. Seed MC: fresh seed moisture content. MeanLG: mean length of germination time. STD MLG: standard deviation of the mean length of germination time. MLG: median length of germination time. Total Germ: total germination percentage. STD Germ: standard deviation of the total germination percentage. Germ. C.V.: coefficient variation of the total germination. First day: first day of germination. Last day: last day of germination. Longevity: number of months that seeds remain viable (total germination >5%) stored at 20ºC in paper bags. "+" is used in cases where longevity assays were ended due to lack of seeds and the last percent of germination was > 5. ISTA (1993) rules were followed.

| Species | Seeds/kg | Seed MC (%) | Mean LG (days) | STD MLG (days) | MLG (days) | Total Germ (%) | STD Germ (%) | Germ. C.V. (%) | First day | Last day | Longevity (months) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Adelia triloba* | 38,873 | 6.43 | 11.2 | 13.7 | 11 | 72 | 9.7 | 13.5 | 8 | 49 | +3 |
| *Albizia adinocephala* | 20,555 | 8.9 | 10.5 | 6.9 | 7 | 77 | 4.2 | 5.5 | 4 | 45 | +7 |
| *Alseis blackiana* | 5,347,593 | | 36 | 23.9 | 24 | 50 | 10 | 20.0 | 24 | 108 | +30 |
| *Amaioua corymbosa* | 105,263 | 59.11 | 58.9 | 30.1 | 52 | 25 | 5 | 20.0 | 38 | 100 | <1 |
| *Anacardium excelsum* | 300 | 34.76 | 11.6 | 4.8 | 14 | 51 | 6.6 | 12.9 | 10 | 17 | 4 |
| *Andira inermis* | 1,616 | 57.2 | 60.3 | 33.6 | 42 | 55 | 27 | 49.1 | 31 | 164 | <1 |
| *Annona spraguei* | 25,363 | 20 | 117.6 | 94.5 | 73 | 14.8 | 1.3 | 8.8 | 24 | 283 | 5 |
| *Antirhea trichantha* | 59,880 | 17.8 | 123.9 | 84.2 | 89 | 29 | 5.5 | 19.0 | 24 | 311 | 26 |
| *Apeiba aspera* | 62,097 | 8.79 | 127.4 | 65.8 | 136 | 9 | 5.5 | 61.1 | 17 | 213 | +6 |
| *Apeiba tibourbou* | 1,545,202 | 6.93 | 31 | 16.5 | 21 | 47 | 14 | 29.8 | 17 | 80 | +15 |
| *Aspidosperma cruenta* | 551 | 79 | 30.5 | 18.3 | 25 | 20 | 2.4 | 12.0 | 13 | 90 | <1 |
| *Beilschmiedia pendula* | | | | | | 90 | | | 10 | 17 | |
| *Brosimun utile* | 182 | 67 | 32.9 | 11.6 | 29 | 77.5 | 7.5 | 9.7 | 17 | 101 | 2 |
| *Bursera simaruba* | 11,376 | 11.41 | 3.8 | 3.8 | 3 | 38 | 3.7 | 9.7 | 6 | 27 | +5 |
| *Byrsonima crassifolia* | | | 167.4 | 8.4 | 164 | 7* | 2.7 | 38.6 | 161 | 184 | |
| *Calophyllum longifolium* | 73 | 41 | 17.1 | 8.3 | 15 | 42 | 11.2 | 26.7 | 5 | 40 | <1 |

**Table 3.** (continued)

| Species | Seeds/kg | Seed MC (%) | Mean LG (days) | STD MLG (days) | MLG (days) | Total Germ (%) | STD Germ (%) | Germ. C.V. (%) | First day | Last day | Longevity (months) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Calycophyllum candidissimum* | 1,149,590 | 10.27 | 11.4 | 1.5 | 7 | 76 | 5.3 | 7.0 | 10 | 45 | +15 |
| *Carapa guianensis* | 20 | 79.7 | 32.7 | 31.7 | 21 | 38 | 9.6 | 25.3 | 12 | 159 | |
| *Cassia grandis* | 2,830 | 18.8 | 8.5 | 8.9 | 9 | 43 | 13 | 30.2 | 8 | 43 | +18 |
| *Castilla elastica* | 2,035 | 45 | 12 | 5.3 | 12 | 86 | 3 | 3.5 | 3 | 38 | <1 |
| *Cedrela odorata* | 36,101 | 38.58 | 9.4 | 2.9 | 7 | 58 | 3.9 | 6.7 | 4 | 46 | 12-15 |
| *Ceiba pentandra* | 14,971 | 7.46 | 4.5 | 0 | 4.5 | 71 | 4.2 | 5.9 | 8 | 8 | +2 |
| *Chrysophyllum cainito* | 2,902 | 41.5 | 22.9 | 7.4 | 20 | 76 | 5.5 | 7.2 | 14 | 76 | 8 |
| *Colubrina glandulosa* | 52,459 | 12.06 | 67.7 | 44 | 61 | 65 | 7.9 | 12.2 | 12 | 166 | +15 |
| *Copaifera aromatica* | 843 | 13.12 | 21 | 3.9 | 23 | 73 | 7.4 | 10.1 | 12 | 33 | +7 |
| *Cordia alliodora* | 215,227 | 9.7 | 17.5 | 0 | 17.5 | 3.5 | 1.3 | 37.1 | 21 | 21 | <1 |
| *Couratari guianensis* | | | | | | 0 | | | | | |
| *Cupania latifolia* | 13,877 | 50.85 | 94.5 | 61.5 | 73 | 58 | 12 | 20.7 | 27 | 300 | 1 |
| *Dalbergia retusa* | 12,315 | 24.3 | 17 | 8.7 | 16 | 77 | 11 | 14.3 | 11 | 60 | 12 |
| *Dendropanax arboreus* | 62,485 | 50 | 23.8 | 5.5 | 21 | 44 | 5.5 | 12.5 | 10 | 66 | <1 |
| *Dialium guianense* | 2,919 | 6.06 | 32.5 | 16.9 | 30 | 2.8 | 1 | 35.7 | 12 | 57 | +2 |
| *Diphysa robinioides* | 59,075 | 11.81 | 11 | 4.7 | 9 | 99 | 0.8 | 0.8 | 5 | 33 | +9 |
| *Dipteryx oleifera* | | 16.42 | 33.3 | 12.8 | 38 | 27 | 13 | 48.1 | 14 | 60 | <1 |
| *Enterolobium cyclocarpum* | 1,238 | 12.03 | 131.2 | 113.4 | 75.5 | 36 | 13 | 36.1 | 4 | 339 | +15 |
| *Enterolobium schomburgkii* | 14,183 | 8.28 | 209.5 | 127.8 | 197 | 38 | 10 | 26.3 | 4 | 397 | +18 |
| *Erythrina fusca* | 2,514 | 14.08 | 25.8 | 21.6 | 16 | 65 | 6 | 9.2 | 5 | 89 | +18 |
| *Faramea occidentalis* | 2,593 | 46.73 | 167.1 | 53.7 | 141 | 66 | 3.4 | 5.2 | 89 | 298 | <1 |

**Table 3** (continued)

| Species | Seeds/kg | Seed MC (%) | Mean LG (days) | STD MLG (days) | MLG (days) | Total Germ (%) | STD Germ (%) | Germ. C.V. (%) | First day | Last day | Longevity (months) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Ficus insipida* | 825,593 | 12.2 | 34.7 | 29.1 | 22 | 18.5 | 4 | 21.6 | 19 | 109 | 7 |
| *Genipa americana* | 7,289 | 36.5 | 28.7 | 12.9 | 24 | 85 | 5.3 | 6.2 | 27 | 99 | 3 |
| *Guarea grandifolia* | 2,034 | 26.7 | | | | 0 | | | | | <1 |
| *Guarea guidonia* | 4,176 | 30.4 | 71.2 | 39.19 | 56 | 49 | 13 | 26.5 | 31 | 241 | <1 |
| *Guazuma ulmifolia* | 224,090 | 11.6 | 52.5 | 40.5 | 35 | 20 | 6.1 | 30.5 | 10 | 143 | +18 |
| *Guettarda foliaceae* | | | 253 | 134 | 134 | 22.5 | 5.3 | 23.6 | 60 | 180 | |
| *Gustavia superba* | 80 | 53.5 | 30.6 | 6.7 | 31 | 76 | 13 | 17.1 | 24 | 45 | 2 |
| *Hampea appendiculata* | 4,860 | 44.9 | 12.5 | 5 | 10 | 50 | 7.9 | 15.8 | 12 | 39 | 2 |
| *Hasseltia floribunda* | 43,589 | 63.3 | 12.8 | 7.5 | 15 | 40 | 12 | 30.0 | 11 | 67 | <-1 |
| *Heisteria concinna* | 3,378 | 30 | 37.9 | 14.8 | 34 | 40 | 5.9 | 14.8 | 24 | 115 | 4 |
| *Hura crepitans* | 829 | 8.7 | 10.8 | 5.8 | 7 | 87 | 4.3 | 4.9 | 10 | 31 | +15 |
| *Hyeronima alcheorneoides* | 123,762 | 28.5 | 61.1 | 35.5 | 52 | 61 | 4.6 | 7.5 | 20 | 223 | 3 |
| *Hymenaea courbaril* | 191 | 15.3 | 21.1 | 8.97 | 17 | 52 | 1.9 | 3.7 | 13 | 62 | 4 |
| *Inga punctata* | 2,425 | 51.65 | 11.5 | 3.4 | 10 | 83 | 13 | 15.7 | 13 | 27 | <1 |
| *Inga spectabilis* | 317 | 46 | 11.2 | 12.7 | 8 | 91 | 2.1 | 2.3 | 5 | 46 | <1 |
| *Jacaranda copaia* | 116,805 | 33.3 | 20.7 | 5 | 22 | 89 | 4.1 | 4.6 | 18 | 39 | +24 |
| *Lacmellea panamensis* | 1,616 | 62.56 | 35.5 | 9.1 | 29 | 75 | 12 | 16.0 | 18 | 109 | 1 |
| *Lafoensia punicifolia* | 18,867 | 12.11 | 3.7 | 1.3 | 4 | 79 | 22.9 | 29.0 | 4 | 14 | +7 |
| *Lindackeria laurina* | 11,312 | 30 | 44.3 | 19.9 | 39 | 39 | 3.9 | 10.0 | 27 | 154 | <-1 |
| *Lonchocarpus latifolius* | 13,757 | 9.63 | 24.4 | 11.1 | 21 | 54 | 11 | 20.4 | 17 | 74 | +10 |
| *Luehea seemannii* | 445,186 | 11 | 122.3 | 99.7 | 76.5 | 38 | 12 | 31.6 | 10 | 311 | +15 |
| *Luehea speciosa* | 216,217 | 18.9 | 31.3 | 26.3 | 14.5 | 22 | 9.7 | 44.1 | 10 | 94 | +18 |
| *Margaritaria nobilis* | 17,884 | 22 | 172.9 | 32.2 | 176 | 5.8 | 3.2 | 55.2 | 117 | 208 | <1 |

**Table 3** (continued)

| Species | Seeds/kg | Seed MC (%) | Mean LG (days) | STD MLG (days) | MLG (days) | Total Germ (%) | STD Germ (%) | Germ. C.V. (%) | First day | Last day | Longevity (months) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Swietenia macrophylla* | 1,351 | 42.2 | 20.9 | 6.36 | 21 | 58 | 3.4 | 5.9 | 17 | 52 | 6 |
| *Tabebuia guayacan* | 51,743 | 14.8 | 24 | 8.41 | 21 | 61 | 5.8 | 9.5 | 24 | 84 | 13 |
| *Tabebuia rosea* | 30,303 | 21.42 | 7.8 | 3.1 | 11 | 83 | 4.8 | 5.8 | 7 | 21 | 11 |
| *Tachigalia versicolor* | 1,140 (samara with wing cut) | 13.2 | 34.9 | 10.97 | 35 | 50 (seeds) | 9.8 | 19.6 | 24 | 66 | 3 |
| *Tapirira guianensis* | 2,598 | 23.6 | 12.7 | 7.6 | 14 | 52.5 | 4.3 | 8.2 | 10 | 82 | <1 |
| *Terminalia amazonia* | 381,862 | 12.9 | 26 | 42.5 | 21 | 3 | 3.3 | 110.0 | 24 | 60 | |
| *Trattinnickinia aspera* | 5,248 £ | 35.1 | 63.6 | 17.8 | 58 | 87 | 14 | 16.1 | 42 | 145 | |
| *Trema micrantha* | 356,697 | 9.5 | 76.6 | 37.1 | 68 | 38 | 2.2 | 5.8 | 36 | 247 | 26 |
| *Trichilia hirta* | 17,391 | 9.2 | 14 | 2.8 | 14 | 83 | 3.5 | 4.2 | 17 | 38 | 12 |
| *Trichilia tuberculata* | 4,606 | 40 | 34.4 | 21.9 | 30 | 11 | 2.6 | 23.6 | 12 | 89 | <1 |
| *Trichospermum galeottii* | 454,545 | 15.64 | 52.6 | 42.6 | 31 | 15 | 4.9 | 32.7 | 20 | 222 | 12 |
| *Triplaris cumingiana* | 33,318 (capsule with wings cut) | 12 | | | | 0 | | | | | |
| *Vantanea depleta* | 259 | 18.1 | 202.8 | 51.9 | 203 | 31 | 12 | 38.7 | 103 | 304 | +5 |
| *Virola sebifera* | 1,933 | 40 | 88 | 18.2 | 84 | 12 | 3 | 25.0 | 55 | 132 | -1 |
| *Virola surinamensis* | 346 | 38.8 | 26.4 | 7.9 | 24 | 45 | 9.3 | 20.7 | 20 | 55 | 10 |
| *Vochysia ferruginea* | 65,805 | 21.2 | 21.8 | 14.3 | 18 | 35 | 4.6 | 13.1 | 11 | 74 | +2 |
| *Xylopia aromatica* | 43,103 | 14.4 | 83.9 | 25 | 83 | 9 | 5.5 | 61.1 | | | +3 |
| *Xylopia frutescens* | 2,088 | 16.65 | 147 | 176 | 100 | 1.25 | 1 | 80.0 | 52 | 282 | -1 |
| *Zanthoxylum panamense* | 28,985 | 21.2 | | | | 0 | | | | | |

*, germination values from assays in 50% of direct sun.

£, data from seeds of a prior collection, which did not germinate a all.

**Table 4.** Germination of species for which pretreatments to break dormancy were applied and of those whose germination increased after dry storage. Differences in germination tested using one-way ANOVA: NS, non significant; *, 0.05≥p >0.01; **, 0.01≥p>0.001; ***, 0.0001 ≥p

| Species | Pretreatment to break dormancy | With pretreatment | | Control | |
|---|---|---|---|---|---|
| | | Germination (%) | MLG (days) | Germination (%) | MLG (days) |
| *Colubrina glandulosa* | Mechanical scarification. Sandpaper seeds gently until the brightness is gone. Germination in shade (3% of direct sun) | 76 ± 10 (NS) | 15.2 ± 4.3 | 65 ± 7.9 | 67.7 ± 44 |
| *Enterolobium cyclocarpum* | Mechanical scarification. Filed seed on lateral side. | 94 ± 3 *** | 4 ± 0 | 36 ± 13 | 131.2 ± 113.4 |
| *E. schcomburgkii* | Mechanical scarification. Filed seed on lateral side. | 79 ± 6.9 *** | 6.8 ±5.8 | 38 ± 10 | 209.5 ± 127.8 |
| *Apeiba aspera* | Submergence in water at 70 ºC for 10 min | 74 ± 12 *** | 49 ± 48 | 9 ± 5.5 | 127.4 ± 65.8. |
| *A. tibourbou* | Submergence in water at 70 ºC for 10 min | 28 ±9.7 (NS) | 24.5 ± 7.3 | 47 ± 14 | 31 ± 16.5 |
| *Luehea seemannii* | Submergence in water at 70 ºC for 10 min. | 62 ** | | 38 ± 12 | 122.3 ± 99.7 |
| *Guazuma ulmifolia* | Submergence in water at 70 ºC for 2 min, followed by washing in running water | 43 ± 12.5 ** | 14 ± 15 | 20 ± 6.1 | 52.2 ± 40.5 |
| *Sapindus saponaria* | Mechanical scarification. Filed testa | 63 | 14.7 ± 24.9 | 5.25 ± 3.5 | 77.6 ± 61.5 |
| *Pseudosamanea guachapele* | Mechanical scarification. Cut testa opposite to micropyle | 84 | 5.4 ± 9.5 | 13 ± 3.9 | 84.3 ± 72 |
| *Cassia grandis* | Mechanical scarification. Filed testa | 44 ± 5.3 (NS) | 7.4 ± 7.4 | 43 ± 13 | 8.5 ± 8.9 |
| *Spondias radlkferii* | One month of dry storage | 41 ± 13 *** | 45.3 ± 21.9 | 5 ± 4.1 | 119.7 ± 84.9 |
| *Spondias mombin* | 30 months of dry storage | 43 ± 12 ** | 17.5 ± 7.4 | 9 ± 5.5 | 79.1 ±110 |

There is a slight trend for seeds dispersed in the early and late rainy season to be larger than those dispersed in the dry season, although the differences were not significant (Tukey HSD test, $p>0.05$) (Fig. 6). All species with seeds > 0.85g are outliers or extremes.

**Moisture content**

Moisture content was determined for fresh seeds of 94 species, and it ranged from 6.06% to 79.7% (Table 3). Frequency distribution of moisture content was right skewed (skewness 0.87), with a mean of 27.7% and a median of 21.3% (Table 4). Thirty-nine species (41.5%) had a moisture content of > 28% (moist seeds), and 55 (58.5%) had a moisture content < 28% (dry seeds). Seed moisture content was weakly correlated with seed weight (Pearson correlation coefficient 0.349, $p<0.01$) (Table 5, Fig. 7), and the majority of seeds < 0.1g was drier than the larger ones (Fig. 8). Species dispersed in the dry season had lower moisture content than those dispersed in the late rainy season (Tukey HSD, $p< 0.05$) (Fig. 9).

**Figure 5.** Seed size distribution for 99 species native to the Panama Canal watershed.

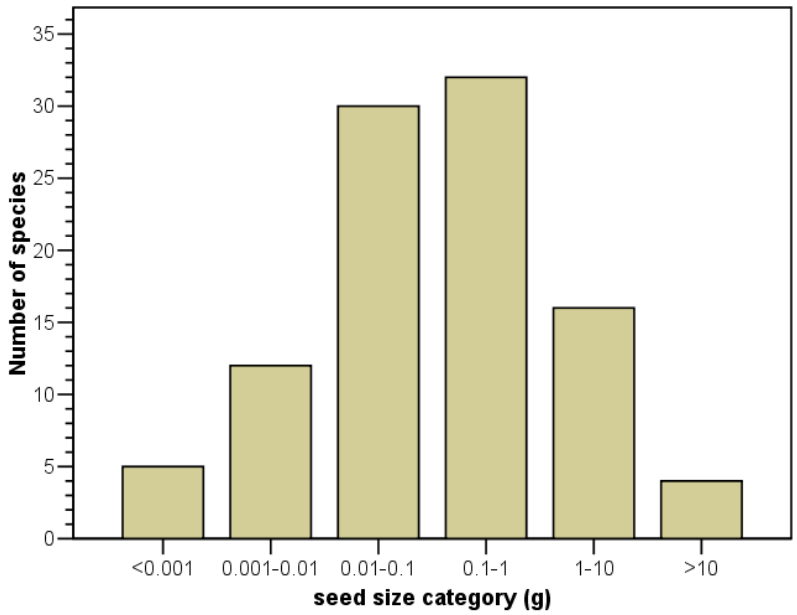


**Figure 6.** Box plots showing median and quartiles of seed weight of species grouped by season of collection. Dry season, January-March; Early rainy season, April –July; Late rainy season, August-December. (Tukey HSD test, p>0.05). All species with seeds > 0.85 g were outliers or extremes**.**

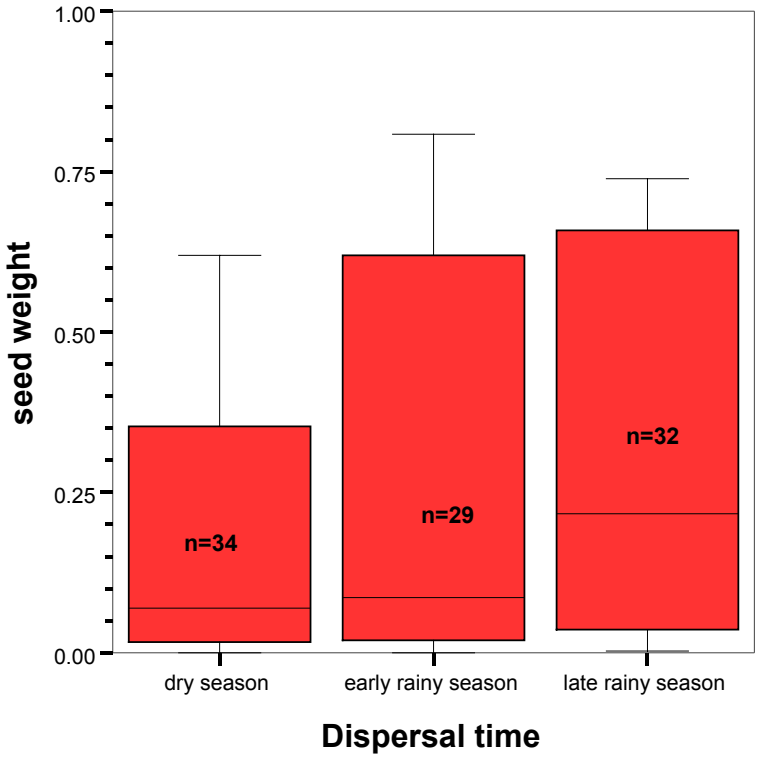



**Figure 7.** Scatter plot for seed weight and seed (or diaspore) moisture content (MC). Pearson correlation coefficient 0.349 (p<0.01)

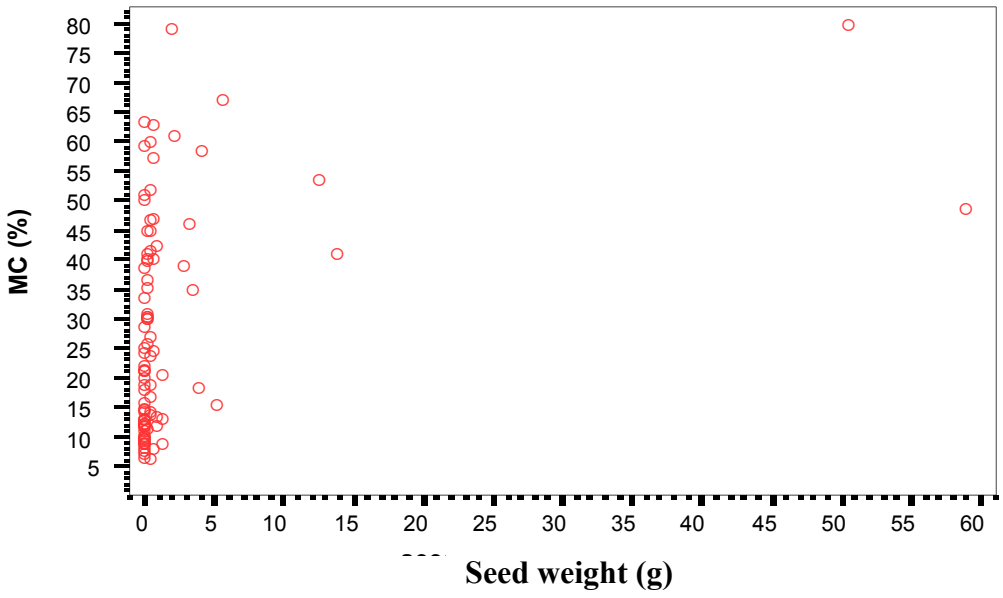


**Table 5**. Descriptive statistics for variables measured in germination studies for 100 species native to the Panama Canal Watershed. MC, seed (or diaspore) moisture content; DST GER, standard deviation of total germination; Mean LG, Mean length of germination period; MLG, median length of germination period; DST MLG, standard deviation of germination period.

| | | seed weight (g) | MC (%) | Total germination percentage (days) | DST GER (%) | Mean LG (days) | DST MLG (days) | MLG (days) | Total length of germination (days) |
|---|---|---|---|---|---|---|---|---|---|
| **N** | | 95 | 94 | 100 | 94 | 94 | 94 | 94 | 94 |
| **Mean** | | 1.96 | 27.73 | 45.37 | 6.80 | 51.92 | 29.10 | 41.97 | 119.14 |
| **Std. Error of Mean** | | .828 | 1.91 | 2.81 | .49 | 5.35 | 3.55 | 4.51 | 9.73 |
| **Median** | | .128 | 21.31 | 46.00 | 5.40 | 31.50 | 13.30 | 24.00 | 83.00 |
| **Std. Deviation** | | 8.07 | 18.48 | 28.13 | 4.71 | 51.86 | 34.41 | 43.73 | 94.33 |
| **Variance** | | 65.20 | 341.43 | 791.29 | 22.22 | 2689.55 | 1183.99 | 1912.78 | 8898.77 |
| **Skewness** | | 6.21 | .87 | -.06 | 1.55 | 1.73 | 1.96 | 1.99 | 1.02 |
| **Std. Error of Skewness** | | .247 | .25 | .24 | .249 | .25 | .249 | .25 | .25 |
| **Kurtosis** | | 39.69 | -.13 | -1.13 | 3.47 | 2.81 | 4.01 | 3.77 | -.05 |
| **Std. Error of Kurtosis** | | .490 | .49 | .48 | .49 | .49 | .49 | .49 | .49 |
| **Range** | | 58.82 | 73.64 | 99.0 | 26.2 | 249.30 | 176.00 | 200.00 | 389 |
| **Minimum** | | .0001 | 6.06 | .0 | .8 | 3.70 | .00 | 3.00 | 8 |
| **Maximum** | | 58.82 | 79.70 | 99.0 | 27.0 | 253.00 | 176.00 | 203.00 | 397 |
| **Percentiles** | **25** | .019 | 12.10 | 20.25 | 3.47 | 16.25 | 6.61 | 14.37 | 45.75 |
| | **50** | .128 | 21.31 | 46.00 | 5.40 | 31.50 | 13.30 | 24.00 | 83.00 |
| | **75** | .60 | 41.00 | 70.75 | 9.85 | 72.55 | 39.52 | 56.50 | 181.00 |

**Figure 8.** Box plots showing median, quartiles, outliers (0), and extremes (*) of seed moisture content (MC) of 94 species grouped by seed size. Letters represent subsets with significant differences. (Tukey HSD test, $p<0.05$)

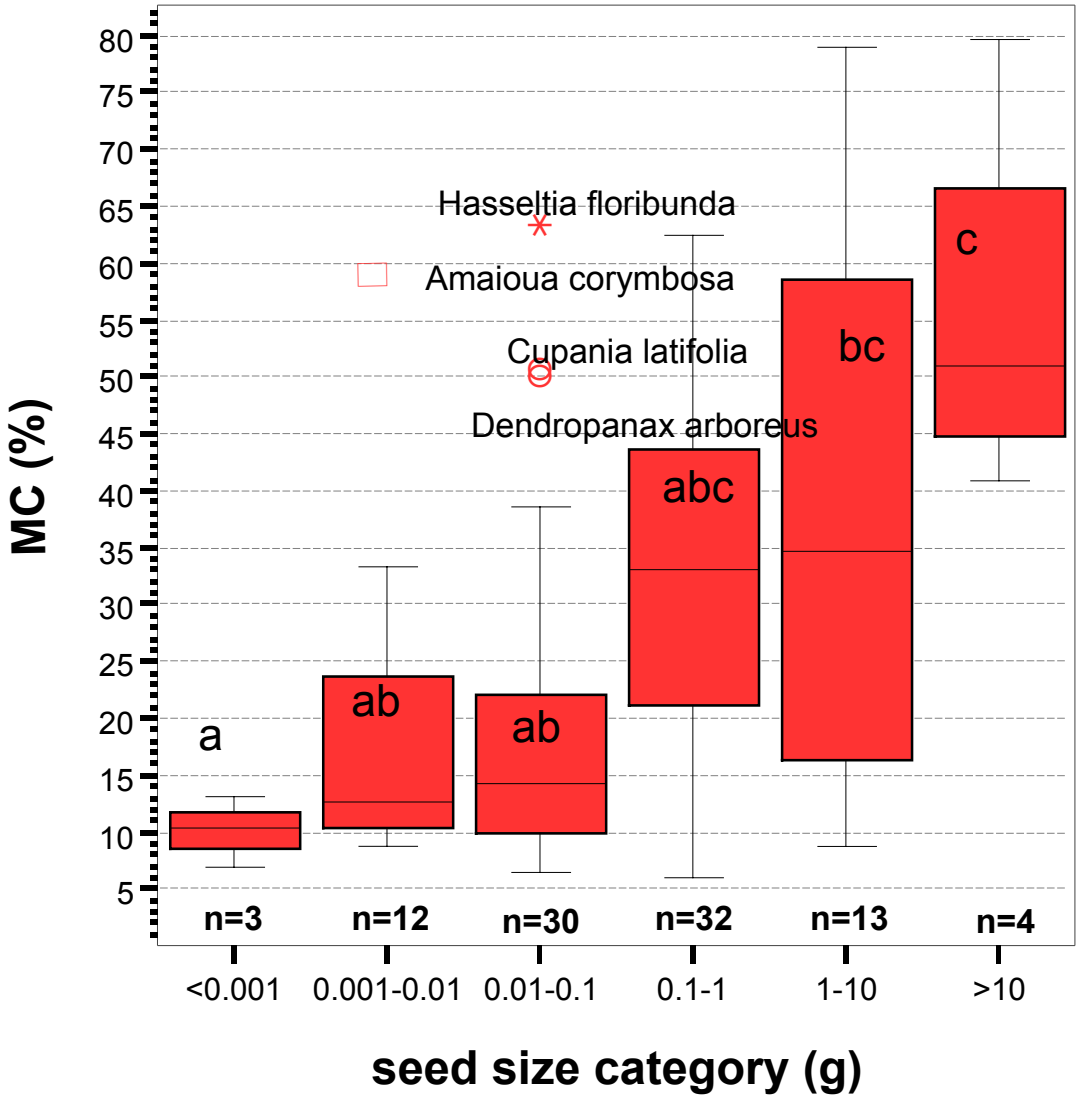
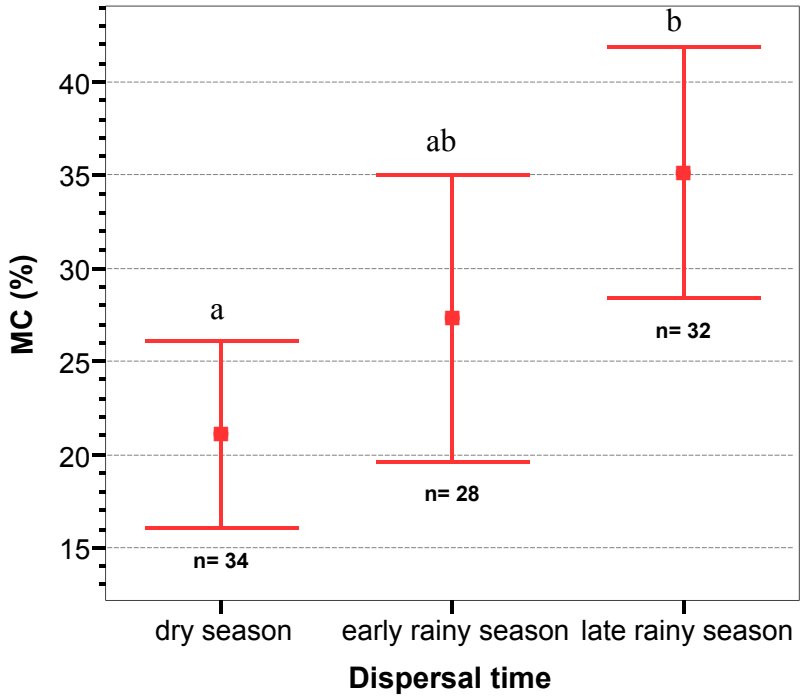


**Figure 9**. Seed (or diaspore) moisture content of species grouped by dispersal season. Dry season, January-March; Early rainy season, April –July; Late rainy season, August-December. Error bars show 95% CI of the mean. Letters indicate subsets with significant difference (Tukey HSD test, $p<0.05$)




**Germination tests**

Seeds of 100 species were evaluated in germination tests. Germination ranged from 0 to 99%, with 46 species (46%) having a germination percentage ≥ 50 (Table 3, Appendix). Standard deviation of total germination ranged from 0 to 27%. Coefficient of variation calculated for those species that germinated ranged from 0.8 to 100%; 47 species (50%) had a coefficient of variation < 15% (Table 3, 5).

Mechanical scarification increased germination of *Colubrina glandulosa* from 44 to 76%, *Sapindus saponaria* from 5.3 to 63%, *Pseudosamanea guachapele* from 13 to 84 %,

*Enterolobium cyclocarpum* from *12 to 94%,* and *E. schkomburgkii* from 8 to 79% . Submergence in warm water (80˚C) increased germination of *Apeiba aspera from 9 to 74%*, *Luehea seemannii from 38 to 62%,* and *Guazuma ulmifolia* from 20 to 46%. However, this same treatment did not improve germination of seeds of *A. tibourbou* (Table 4).

Table 5 summarizes statistics and Table 6 correlations for seed characteristics and germination variables. With the exception of total germination percentage, all variables have a right-skewed distribution. Although correlated between themselves, seed weight and seed moisture content are not correlated with any of the germination variables. Mean, median, and standard deviation of germination length and coefficient of variation of total germination percentage are positively correlated, and they are negatively correlated with total percent germination.

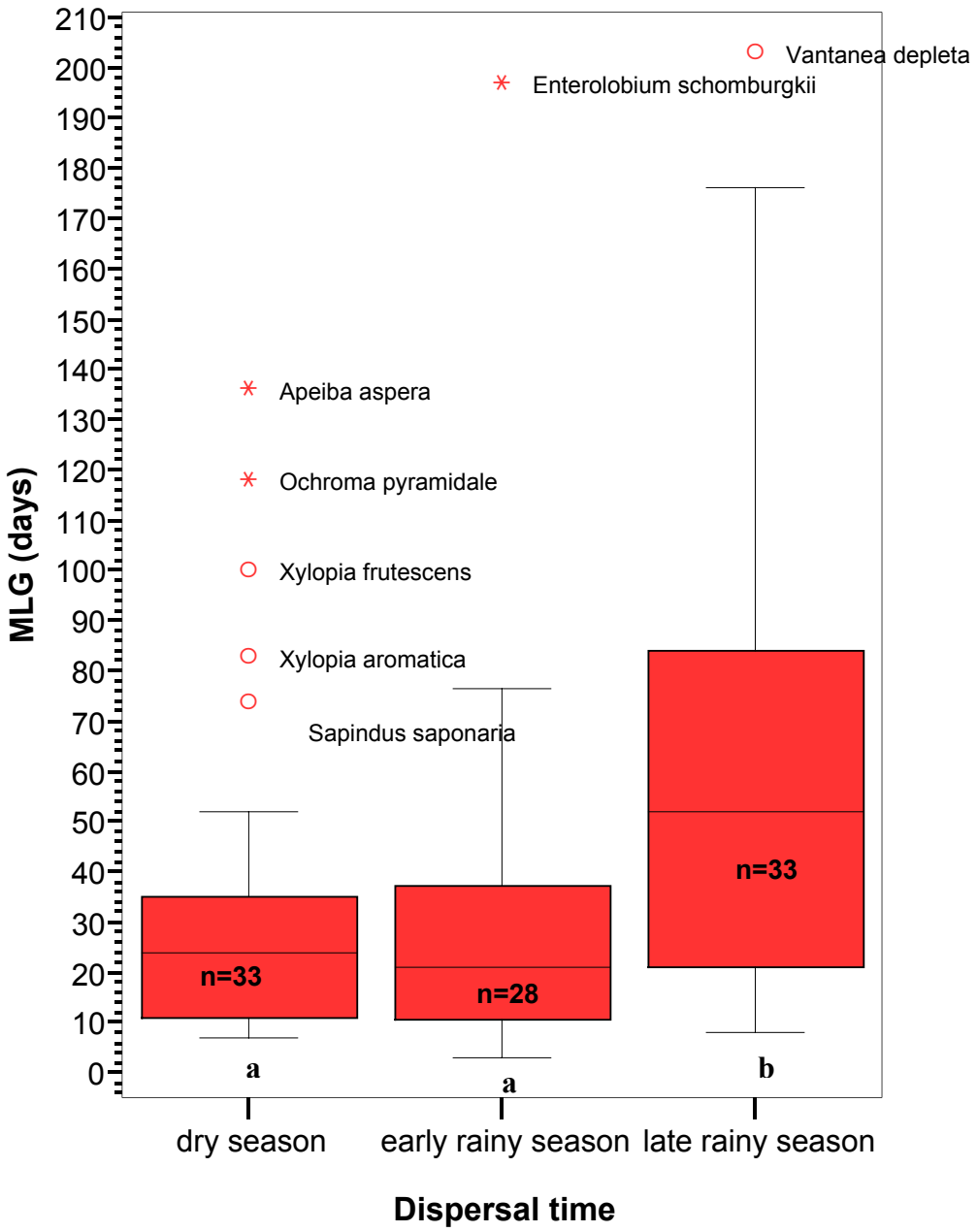
Mean length of germination period (MeanLG) ranged from 3.7 to 253 days, with a mean of 51.92 days and a median of 31.5 days. Median length of germination period (MLG) ranged from 3 to 203 days, with a mean of 41.97 days and a median of 24 days. The Pearson correlation coefficient between mean and median length of germination period was 0.91 ($p<0.01$). Total length of germination period ranged from 8 to 397 days, with a mean of 119 days and a median of 83 days. The standard deviation of length of germination period ranged from 0 to 176 days, with a mean of 29.10 days and a median of 13.3 days. The Pearson correlation coefficient between standard deviation of length of germination period (STD MLG) and total length of germination was 0.84 ($p<0.01$) (Table 5, 6). Forty-five species (55.3%) had an MLG > 30 days, and only 12 species had an MLG ≥120 days. Species dispersed in the late rainy season had a higher MLG than those dispersed in the early rainy and dry seasons (Fig 10). Forty-eight species (51%) had uniform germination (i.e. STD MLG ≤14 days) (Table 3).

**Table 6.** Pearson correlation coefficients between variables measured in germination studies for 100 species native to the Panama Canal Watershed. Significant correlations are highlighted in boxes colored in green. MC, seed (or diaspore) moisture content; Mean LG, Mean length of germination period; MLG, median length of germination period; DST MLG, standard deviation of length of germination period; N, sample size. Green boxes are those with significant correlation.

| | | MC (%) | Mean LG | DST MLG | Total germination percentage | Coefficient variation of total germination | MLG | Total length of germination |
|---|---|---|---|---|---|---|---|---|
| seed weight | Pearson Correlation | .349(**) | -.060 | -.051 | .008 | .004 | -.042 | -.041 |
| | Sig. (1-tailed) | .000 | .286 | .316 | .468 | .969 | .346 | .351 |
| | N | | 91 | 91 | 95 | 91 | 91 | 90 |
| MC (%) | Pearson Correlation | | -.075 | -.090 | .128 | .073 | .001 | -.009 |
| | Sig. (1-tailed) | | .241 | .198 | .109 | .495 | .497 | .467 |
| | N | | 90 | 90 | 94 | 90 | 90 | 89 |
| MLG | Pearson Correlation | | | .793(**) | -.454(**) | .349(**) | .909(**) | .843(**) |
| | Sig. (1-tailed) | | | .000 | .000 | .001 | .000 | .000 |
| | N | | | 94 | 94 | 94 | 94 | 93 |
| DST MLG | Pearson Correlation | | | | -.452(**) | .438(**) | .674(**) | .838(**) |
| | Sig. (1-tailed) | | | | .000 | .000 | .000 | .000 |
| | N | | | | 94 | 94 | 94 | 93 |
| Total germination percentage | Pearson Correlation | | | | | -.669(**) | -.412(**) | -.388(**) |
| | Sig. (1-tailed) | | | | | .000 | .000 | .000 |
| | N | | | | | 94 | 94 | 94 |
| Coefficient variation of total germination | Pearson Correlation | | | | | | .0309(**) | .291(**) |
| | Sig. (1-tailed) | | | | | | .002 | .005 |
| | N | | | | | | 94 | 93 |
| Median length of germination | Pearson Correlation | | | | | | | .782(**) |
| | Sig. (1-tailed) | | | | | | | .000 |
| | N | | | | | | | 93 |

** Correlation is significant at the 0.01 level (1-tailed).
* Correlation is significant at the 0.05 level (1-tailed).

**Figure 10.** Box plots showing median, quartiles, outliers (o), and extremes (*) of median time of germination for the species grouped by season of seed dispersal. MLG, mean length of germination period; DS, dry season (January-March); ERS, early rainy season (April-June); LRS, late rainy season (July-December). Letter indicates subsets with significant difference (Tukey HSD test, $p<0.05$)



**Longevity studies**

Ninety species were evaluated for seed longevity, which ranged from 0.5 to 36 months (Table 3). *Byrsonyma crassifolia, Cordia alliodora, Guarea grandifolia, Margaritaria nobilis Protium panamense, Terminalia amazonia, Xylopia aromatica*, and *X. frutescens* had initial germination <10%. *Byrsonima. crassifolia, C. alliodora*, and *X. aromatica* were considered as long-lived, and *Carapa guianense* and *G. grandifolia* were considered to be very-short lived based on information from the literature (Geilfus, 1994; Salazar, 2000; Tweddle et al., 2003a). A total of 89 species was assigned to a category: 54 (60.7%) of the species had long lived seeds, 12 (13.5%) short-lived seeds, and 23 (25.8%) very short lived seeds. Seed moisture content increased significantly from long-lived seeds to very short live ones (Fig. 11). Short and very short-lived seeds tend to be larger, but the differences are not significant differences (Tukey HSD test, $p > 0.05$) (Fig. 12). The proportion of very short-lived seeds increased in the rainy season (Fig. 13).

In 88 of the 90 species, viability decreased with time of storage. However, seeds of *Spondias mombin* and *S. raldkoferii* had higher germination percentages and germinated faster after dry storage at 20ºC than fresh seeds (Table 4). Germination of *S. raldkoferii* increased from 5 to 41% during 1- month of dry storage ($p < 0.001$), and those of *S. monbin* increased significantly from 2% for fresh seeds up to 43% during 30 months ($p<0.01$) (Table 4, Fig. 14).

**Nursery management constraints**

The number of species whose peak of germination fell in each month is shown in Figure 15. The months with the most species in their germination peak, March and August, coincided with peaks of seed collection.

**Figure 11.** Box plots showing median, quartiles, outliers (o), and extremes (*) of seed moisture content of study species grouped by longevity category. Very short, ≤ 1 month for germination to decrease to less than 5%; short, 1-4 months; long, >4 months. Letters indicate subsets with significant difference (Tukey HSD test, $p<0.05$)

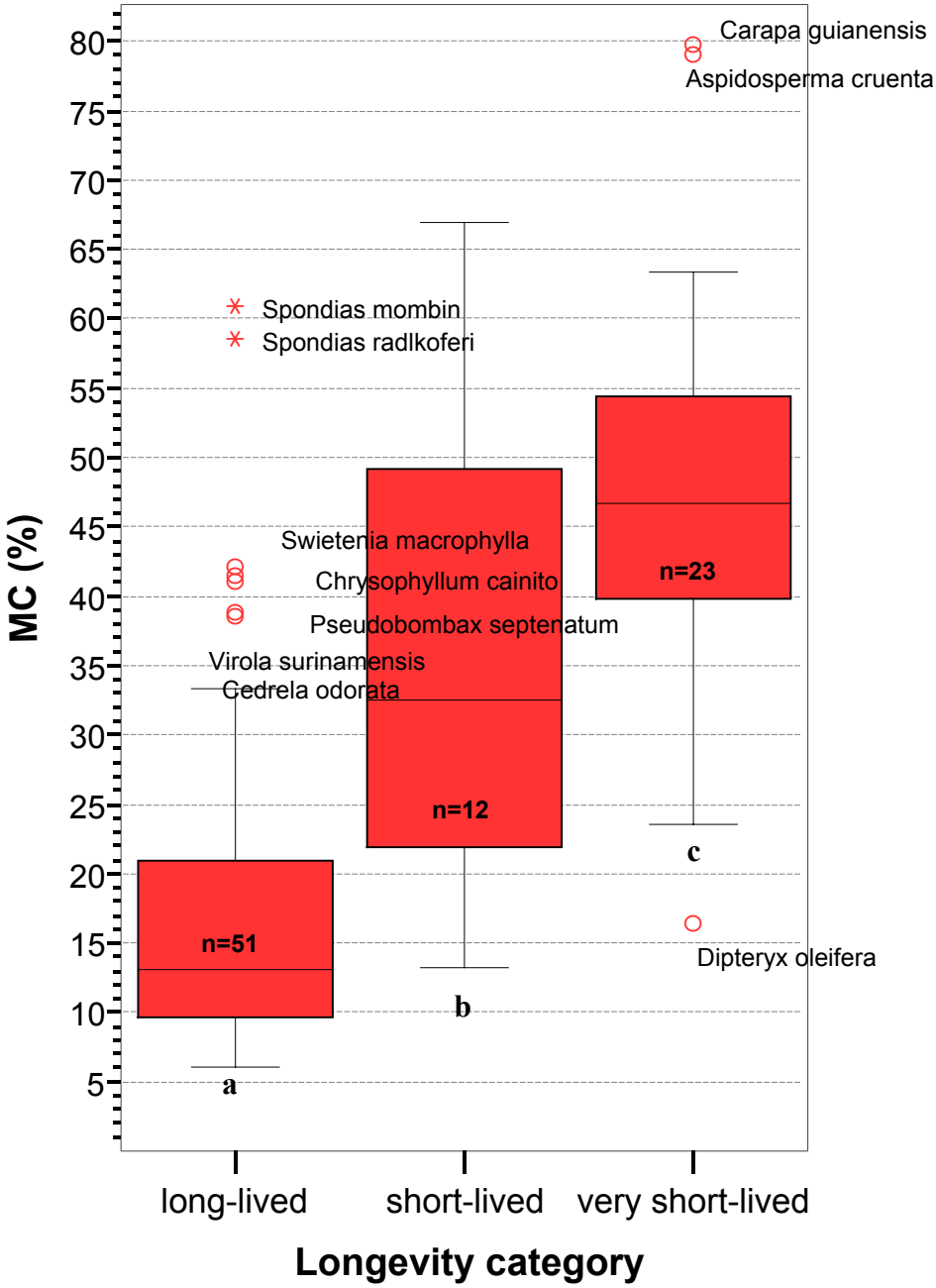


**Figure 12.** Box plots showing median, quartiles, outliers (o), and extremes (*) of seed weight of study species grouped by longevity category. Very short, ≤ 1 month for germination to decrease to less than 5%; short, 1-4 months; long, >4 months. (Tukey HSD test, p> 0.05).

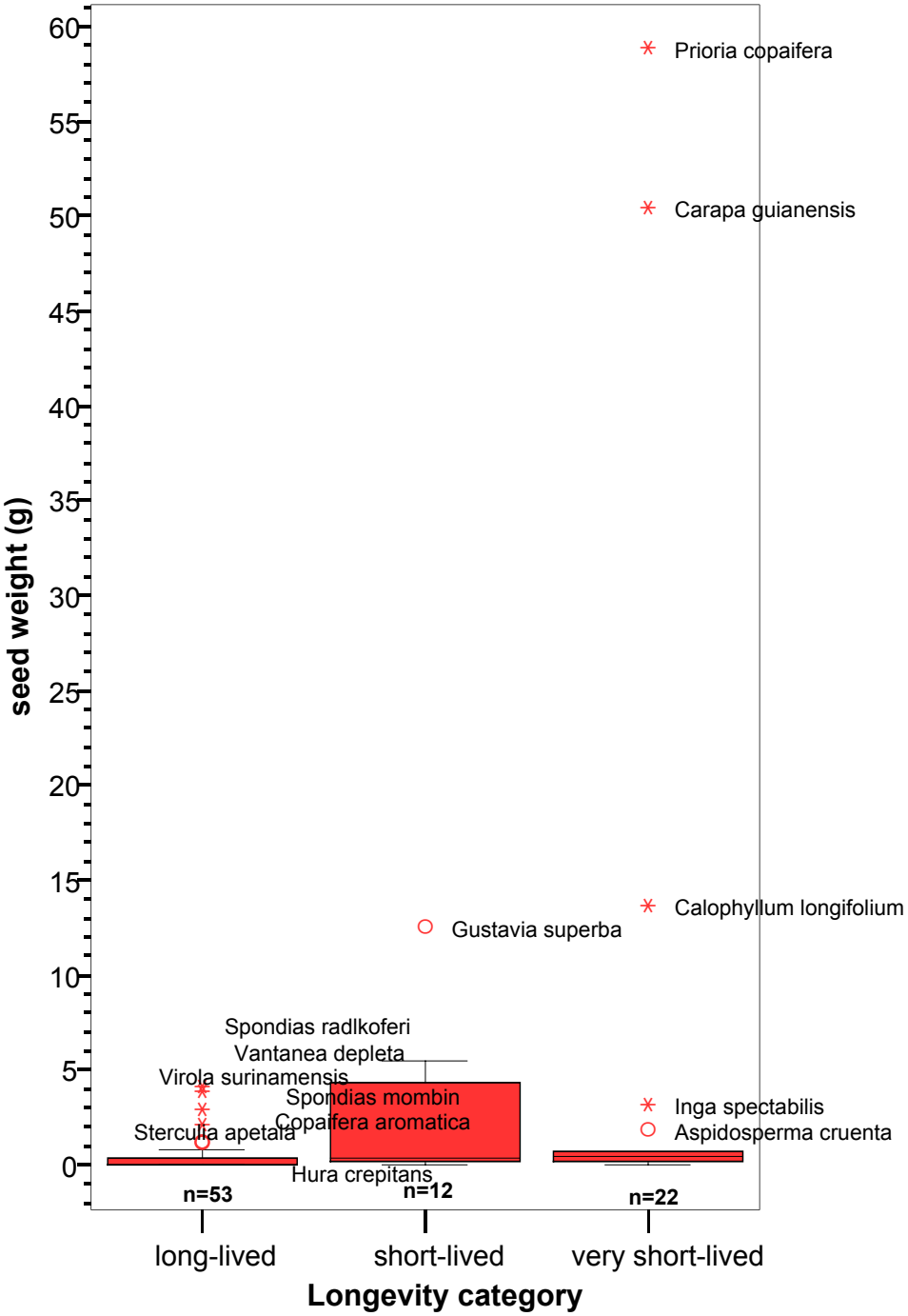


**Figure 13.** Longevity of species grouped by dispersal time. Dry season (January-March); Early rainy season (April-June); Late rainy season (July-December). Dots show means, and error bars show 95% confidence interval of mean. Very short, ≤ 1 month for germination to decrease to less than 5%; short, 1-4 months; long, >4 months.

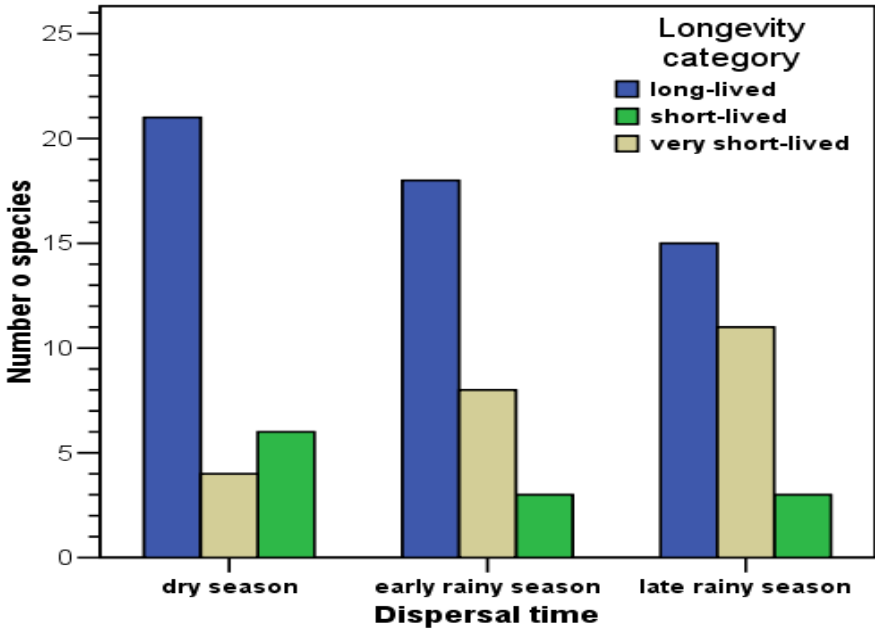



**Figure 14.** Germination of seeds of *Spondias monbin* after different periods of storage in paper bags at 20ºC and 60% RH. Linear regression ($R^2$=0.567, p<0.0001), B=1.463, ß=0.7528, SE=0.1334

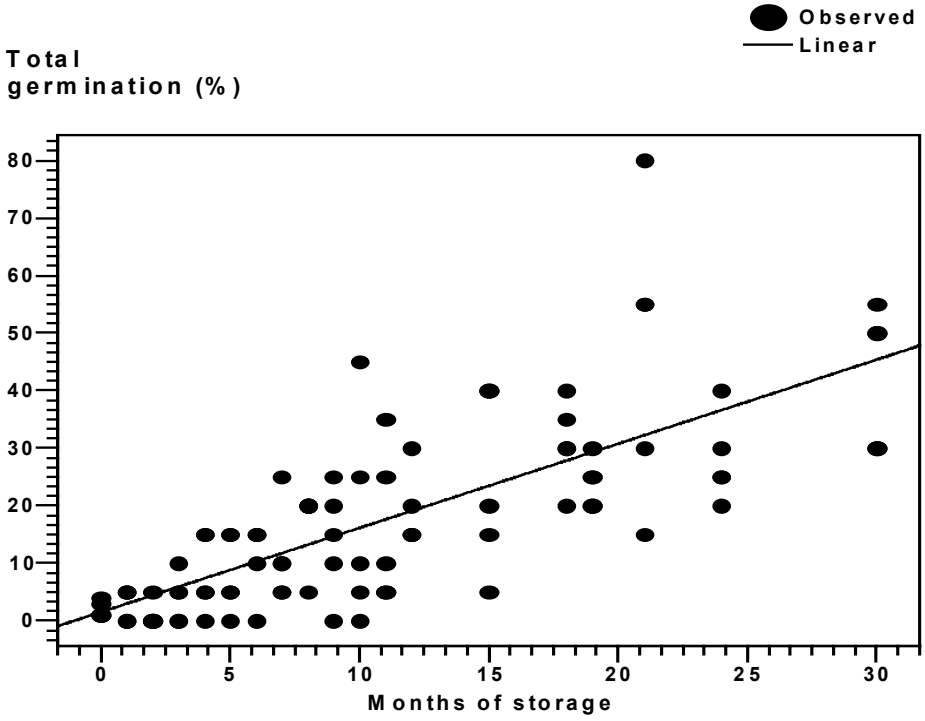
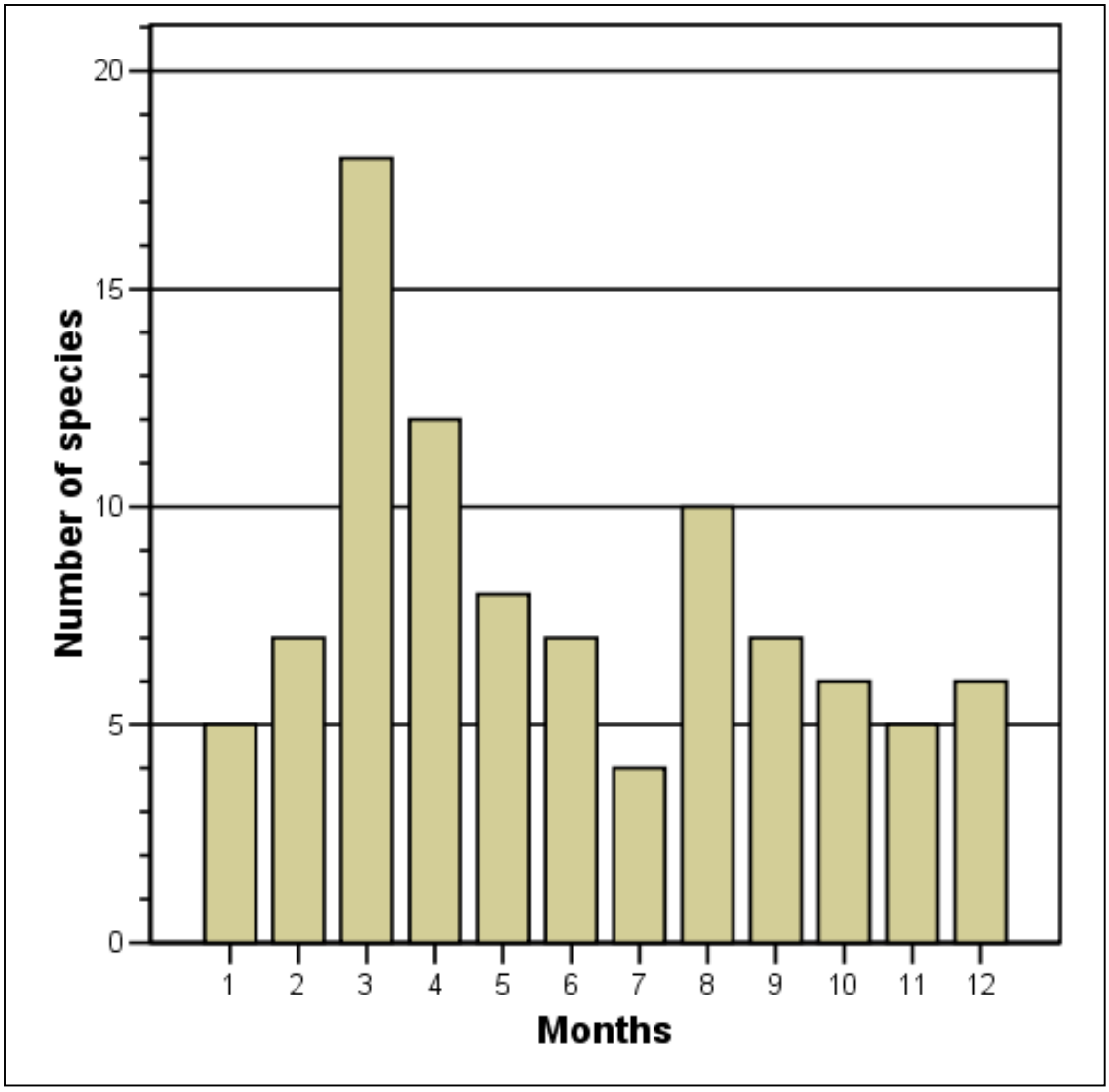


**Fig. 15.** Number of species whose peak of germination (calculated based on month of seed collection and median length of germination period) of non-pretreated seeds occurred in each month.



## II. ASSIGNMENT TO SEED DORMANCY CLASS:

Class of dormancy was assigned to fresh seeds of 94 of the 100 species based on median time of germination (MLG), permeability (or not) of the seed coat to water, type of embryo, and/or taxonomic relationships. No seeds of five species germinated (*Couratari guianensis, Guarea grandifolia, Platysmiscium pinnatum, Triplaris cummigiana,* and *Zanthoxyllum panamense*). Seeds of *Terminalia amazonia* and *Cordia alliodora* appeared not to be viable, probably due to empty seeds, which is reported to be a common problem in these species (Flores, 2003, Salazar, 2000). Germination reports for *T. amazonia* are insufficient to assigned dormancy class (Flores, 2003), and *C. alliodora* was considered non- dormant based on the literature (Salazar, 2000). Forty-nine species (52.1%) were non-dormant (MLG≤ 30 days), and 45 (47.9%) were dormant (MLG> 30 days) (Table 3). Although I do not have data to calculate MLG for *Beilschmedia pendula*, its seeds were considered to be non-dormant since the germination period ended in less than 30 days.

Twenty-three (24.5%) of the species had physiological dormancy (PD), seven (7.4%) morphophysiological dormancy (MDP), two (2.1%) morphological dormancy, and 13 (13.8%) physical dormancy (PY) (Table 7, Fig. 16). No seeds had combinational (PY+PD) dormancy.

### Species with physical dormancy

I conducted imbibition tests for 12 species. Six of them have impermeable seed coats (*Apeiba aspera, Colubrina glandulosa, Enterolobium cyclocarpum, E. schomburgkii, Luehea seemannii, Ormosia macrocalyx)* (Fig. 17-22). *Ficus insipida, Guarea guidonea,* and *Trema micrantha* and *Amaioua corymbosa* had permeable testa (Fig. 23-26), and *Heisteria concinea Andira inermis* had a permeable endocarp (Fig. 27-28). A small proportion of the seeds of *A. aspera* and *E. schomburgkii* were permeable (2 % and 15 %, respectively). During imbibition the seed coat of *A. aspera* forms a mucilage that surrounds the seed. Thus, to test the actual imbibition through the testa I imbibed the seeds for 12 hours and gently scrubbed as much mucilage from the seeds as possible. Then, I let the seeds dry for 12 hours, after which I ran the imbibition test (Fig. 29).

Pretreatments increased germination significantly in fresh seeds of seven of the species (*Enterolobium cyclocarpum, E. schomburgkii, Luehea seemannii, Guazuma ulmifolia,*

*Pseudosamanea guachapele, Colubrina glandulosa*, and *Apeiba aspera)*. Germination of seeds of *Luehea speciosa* decreased after 4-5 months of storage and increased significantly with pretreatment in the following months. Germination percentages of seeds of *Apeiba tibourbou* and *Cassia grandis* did not vary significantly with pretreatments (see cumulative germination curves in appendix).

*Pseudosamanea guachapele* and *Dialium guianense* (Fabaceae) with MLG>30 days, and *Apeiba tibourbou* and *Luehea speciosa* (Tiliaceae) with MLG<30days, have been considered to have physical dormancy at least in some seeds per lot, inferred from my germination test results, information in the literature, and characteristics of seeds in that family and/or genus (Baskin et al., 2000). Germination of both species in the family Tiliaceae increased significantly with pretreatment. *Apeiba tibourbou* germinated to a higher percentage when treated with sulfuric acid (Acuña and Garwood, 1987), and germination of stored seeds of *Luehea speciosa* increased after immersion in hot water (see appendix).

Physical dormancy was assigned to three species from information in the literature. *Ochroma pyramidale* (Bombacaceae), *Trichospermum galeottii* (Tiliaceae) and *Guazuma ulmifolia* (Sterculiaceae) have been reported to have impermeable seed coats (Acuña and Garwood, 1987), and their MLG was > 30 days.

**Species with physiological dormancy**

*Andira inermis, Trema micrantha, and Guarea guidonea* had MLG>30 days, permeable seed coats, and fully developed embryos. Thus they have physiological dormancy (Fig. 30). Nineteen species with MLG > 30 days were not available for testing permeability or for determining whether the embryo was underdeveloped or fully developed. However, all of these species were considered to have physiological dormancy since they belong to families known to have fully developed embryos and water-permeable seed coats (Baskin and Baskin, 1998)(Table 4). Seeds of *Byrsonima crassifolia* and *Cordia alliodora* germinated to very low percentages (7 and 3.5 respectively), and were assigned to physiological dormancy based in my germination data and information in the literature (Correa A., 2003, Geilfus, 1994, Vega et al., 1983, Salazar, 2000).

*Prioria copaifera, Tachigalia versicolor*, and *Dipteryx oleifera* (Fabaceae) belong to families known to have fully developed embryos and both physical and physiological

dormancy (Baskin and Baskin, 1998). They were assigned to have physiological dormancy based in their short longevity and potential recalcitrant behavior, which is inconsistent with the presence of physical dormancy (Tweddle et al. 2003b).

*Spondias monbin* and *S. raldkoferii* (Anacardiaceae) also belong to a family known to have fully developed embryos and reported to have both physical and physiological dormancy. They were assigned to have physiological dormancy based on the high moisture content of fresh seeds, which is inconsistent with the presence of physical dormancy, and on the fact that physical dormancy is not known in tribe Spondidae of Anacardiaceae (Baskin et al., 2000).

**Species with morphological dormancy**

*Dendropanax arboreus* (Araliaceae) and *Virola surinamensis* (Myristicaceae) were assigned to morphological dormancy based on the mean time of germination (MLG<30 days) and on the fact that these families have underdeveloped embryos (Baskin and Baskin, 1998).

**Species with morphophysiological dormancy**

*Annona spraguei, Xylopia frutescesns,* and *X. aromatica* (Annonaceae), *Virola sebifera* (Myristicaceae), and *Schefflera morototoni* (Araliaceae) were assigned to morphophysiological dormancy based on the mean time of germination (MLG > 30 days) and on the fact that these families have underdeveloped embryos (Baskin and Baskin, 1998). *Heisteria concinea* (Olacaceae) and *Amaioua corymbosa* (Rubiaceae) had permeable seeds coats and underdeveloped embryos and MLG > 30 days; thus, they were assigned to have morphophysiological dormancy (Fig. 31, 32)

**Characteristics of seeds with each kind of dormancy**

Given the small number of species with MPD (7) and MD (2), species in both classes were considered as one group for the purpose of comparison between classes of dormancy.

Seeds of eight of the 16 species (50%) with a mass of 1-10g had PD, seven had ND, and one had MPD. Box-plots for seed weight in each dormancy class in Fig. 33 show that seeds with PY have significantly smaller seeds, and seeds with ND, PD, and MPD tend to be larger than those with PY (Tukey HSD test, $p<0.05$). *Virola surinamensis* (2.9 g) is an extreme case in the MPD class. Seeds that weigh >2.5 g are extremes or outliers in the ND category

(*Aspidosperma cruenta, Inga spectabilis, Anacardium excelsum, Hymenaea courbaril, Brosimun utile, Calophyllum longifolium,* and *Carapa guianensis*); seeds that weigh >3g are outliers or extremes in the PD category (*Vantamea depleta, Spondias raldkoferii, Gustavia superba*, and *Proiria copaifera*); and seeds that weigh >0.1g are extremes in the PY category (*Dialium guianense, Enterolobium cyclocarpum*, and *Ormosia macrocalyx*) (Fig. 33).

For 89 species to which dormancy class was assigned, we know the moisture content of the fresh seed. Seeds with PY have lower moisture content than those in the other dormancy classes (Tukey HSD Test, $p<0.05$) (Fig. 34).

The majority of species with physiologically dormant seeds are dispersed in the late rainy season (60.9%), those with physical dormancy mainly in the dry and early rainy season (84.7%), and those that are nondormant year-round (Fig. 35). Differences in the distribution of dormancy classes between gap-specialist and generalist species are not significant (Chi square >0.05) (Fig. 36).

There was a statistically significant difference in class of dormancy between large trees (≥20 m in height), mid-size trees (10-20 m), and understory trees (4-10 m) (Chi-Square < 0.05) (Fig. 37). The majority of large trees (63%) have non-dormant seeds followed by those with PD (18%), PY (14%), MD (3%), and MPD (2%). Thirty five percent of mid-size trees have non-dormant seeds, 31% PD, 19% MPD, and 15% PY. Seeds of four of the six understory trees have PD (67%), one ND, one MPD, and none PY or MD.

I had information on longevity in storage and class of dormancy for 88 species. All seeds with PY are long-lived, the majority of non-dormant seeds are long lived (61.7%), and the majority of seeds with PD (55%) and with MD or MPD (62.5%) are short or very short lived (Fig. 38).

**Table 7.** Class of dormancy and storage behavior assigned to 94 species native to the Panama Canal Watershed. ND, non-dormant; PD, physiological dormancy; PY, physical dormancy; MD, morphological dormancy; MPD, morphophysiological dormancy; MLG, median length of germination period; GER, final germination; Longevity category: V, very short-lived (<1 month); S, short-lived (1-4 months), L, long-lived (>4 months to decrease germination to <5%).

| FAMILY | Species | GER (%) | MLG (days) | Class of dormancy | Longevity category |
|---|---|---|---|---|---|
| Non-dormant species | | | | | |
| ANACARDIACEAE | *Anacardium excelsum* | 51 | 14 | ND | S |
| ANACARDIACEAE | *Tapirira guianensis* | 52.5 | 14 | ND | V |
| APOCYNACEAE | *Aspidosperma cruenta* | 20 | 25 | ND | V |
| APOCYNACEAE | *Lacmellea panamensis* | 75 | 29 | ND | V |
| BIGNONIACEAE | *Jacaranda copaia* | 89 | 22 | ND | L |
| BIGNONIACEAE | *Tabebuia guayacan* | 61 | 21 | ND | L |
| BIGNONIACEAE | *Tabebuia rosea* | 83 | 11 | ND | L |
| BOMBACACEAE | *Ceiba pentandra* | 71 | 4.5 | ND | L |
| BOMBACACEAE | *Pachira quinata* | 44 | 10 | ND | L |
| BOMBACACEAE | *Pseudobombax septenatum* | 86 | 9 | ND | L |
| BOMBACACEAE | *Quararibea asterolepis* | 38 | 26 | ND | V |
| BORAGINACEAE | *Cordia alliodora* | 3.5 | 18 | ND | L |
| BURSERACEAE | *Bursera simaruba* | 38 | 3 | ND | L |
| BURSERACEAE | *Protium panamense* | 7 | 30 | ND | --- |
| BURSERACEAE | *Protium tenuifolium* | 85 | 8 | ND | S |
| CLUSIACEAE | *Calophyllum longifolium* | 42 | 15 | ND | V |
| EUPHORBIACEAE | *Adelia triloba* | 72 | 11 | ND | L |
| EUPHORBIACEAE | *Hura crepitans* | 87 | 7 | ND | L |
| FABACEAE-CAES | *Cassia grandis* | 43 | 9 | ND | L |
| FABACEAE-CAES | *Copaifera aromatica* | 73 | 23 | ND | L |
| FABACEAE-CAES | *Hymenaea courbaril* | 52 | 17 | ND | S |
| FABACEAE-FAB | *Dalbergia retusa* | 77 | 16 | ND | L |
| FABACEAE-FAB | *Diphysa robinioides* | 99 | 9 | ND | L |
| FABACEAE-FAB | *Erythrina fusca* | 65 | 16 | ND | L |
| FABACEAE-FAB | *Lonchocarpus latifolius* | 54 | 21 | ND | L |
| FABACEAE-FAB | *Pterocarpus rohrii* | 77 | 21 | ND | L |
| FABACEAE-MIM | *Albizia adinocephala* | 77 | 7 | ND | L |
| FABACEAE-MIM | *Inga punctata* | 83 | 10 | ND | V |
| FABACEAE-MIM | *Inga spectabilis* | 91 | 8 | ND | V |
| FLACOURTIACEAE | *Hasseltia floribunda* | 40 | 15 | ND | V |

**Table 7.** (continued)

| FAMILY | Species | GER (%) | MLG (days) | Class of dormancy | Longevity category |
|---|---|---|---|---|---|
| LAURACEAE | *Beilshmedia pendula* | 90 | -- | ND | -- |
| LAURACEAE | *Phoebe cinnamomifolia* | 47 | 18 | ND | V |
| LYTHRACEAE | *Lafoensia punicifolia* | 79 | 4 | ND | L |
| MELASTOMATACEAE | *Miconia argentea* | 57 | 24 | ND | L |
| MALVACEAE | *Hampea appendiculata* | 50 | 10 | ND | S |
| MELIACEAE | *Carapa guianensis* | 38 | 21 | ND | V |
| MELIACEAE | *Cedrela odorata* | 58 | 7 | ND | L |
| MELIACEAE | *Swietenia macrophylla* | 58 | 21 | ND | L |
| MELIACEAE | *Trichilia hirta* | 83 | 14 | ND | L |
| MELIACEAE | *Trichilia tuberculata* | 11 | 30 | ND | V |
| MORACEAE | *Brosimun utile* | 77.5 | 29 | ND | S |
| MORACEAE | *Castilla elastica* | 86 | 12 | ND | V |
| MORACEAE | *Ficus insipida* | 18.5 | 22 | ND | L |
| RUBIACEAE | *Alseis blackiana* | 50 | 24 | ND | L |
| RUBIACEAE | *Calycophyllum candidissimum* | 76 | 7 | ND | L |
| RUBIACEAE | *Genipa americana* | 85 | 24 | ND | S |
| SAPOTACEAE | *Chrysophyllum cainito* | 76 | 20 | ND | L |
| STERCULIACEAE | *Sterculia apetala* | 37 | 9 | ND | L |
| VOCHYSIACEAE | *Vochysia ferruginea* | 35 | 18 | ND | L |
| Dormant species | | | | | |
| ANACARDIACEAE | *Spondias radlkoferi* | 5 | 83 | PD | L |
| ANACRADIACEAE | *Spondias mombin* | 9 | 148 | PD | L |
| BURSERACEAE | *Trattinnickinia aspera* | 87 | 58 | PD | -- |
| EUPHORBIACEAE | *Hyeronima alcheorneoides* | 61 | 52 | PD | S |
| EUPHORBIACEAE | *Margaritaria nobilis* | 5.8 | 176 | PD | ---- |
| EUPHORBIACEAE | *Sapium glandulosum* | 70 | 31 | PD | L |
| FABACEAE-CAES | *Prioria copaifera* | 50 | 32 | PD | V |
| FABACEAE-CAES | *Tachigalia versicolor* | 50 | 35 | PD | S |
| FABACEAE-FAB | *Andira inermis* | 55 | 42 | PD | V |
| FABACEAE-FAB | *Dipteryx oleifera* | 27 | 38 | PD | V |
| FLACOURTIACEAE | *Lindackeria laurina* | 39 | 39 | PD | V |
| HUMIRIACEAE | *Vantanea depleta* | 31 | 203 | PD | L |
| LECYTHIDACEAE | *Gustavia superba* | 76 | 31 | PD | S |
| MALPIGHIACEAE | *Byrsonima crassifolia* | 7 | 164 | PD | L |
| MELASTOMATACEAE | *Miconia minutiflora* | 45 | 51 | PD | L |
| MELIACEAE | *Guarea guidonia* | 49 | 56 | PD | V |
| RUBIACEAE | *Antirhea trichantha* | 29 | 89 | PD | L |
| RUBIACEAE | *Faramea occidentalis* | 66 | 141 | PD | V |

**Table 7.** (continued)

| FAMILY | Species | GER (%) | MLG (days) | Class of dormancy | Longevity category |
|---|---|---|---|---|---|
| RUBIACEAE | *Guettarda foliaceae* | 22.5 | 134 | PD | -- |
| RUBIACEAE | *Posoqueria latifolia* | 68 | 86 | PD | S |
| SAPINDACEAE | *Cupania latifolia* | 58 | 73 | PD | V |
| SAPINDACEAE | *Sapindus saponaria* | 5.25 | 74 | PD | L |
| ULMACEAE | *Trema micrantha* | 38 | 68 | PD | L |
| BOMBACACEAE | *Ochroma pyramidale* | 21 | 118 | PY | L |
| FABACEAE-CAES | *Dialium guianense* | 2.8 | 30 | PY | L |
| FABACEAE-FAB | *Ormosia macrocalyx* | 49 | 59 | PY | L |
| FABACEAE-MIM | *Enterolobium cyclocarpum* | 36 | 76 | PY | L |
| FABACEAE-MIM | *Enterolobium schomburgkii* | 38 | 197 | PY | L |
| FABACEAE-MIM | *Pseudosamanea guachapele* | 13 | 81 | PY | L |
| RHAMNACEAE | *Colubrina glandulosa* | 65 | 61 | PY | L |
| STERCULIACEAE | *Guazuma ulmifolia* | 20 | 35 | PY | L |
| TILIACEAE | *Apeiba aspera* | 9 | 136 | PY | L |
| TILIACEAE | *Apeiba tibourbou* | 47 | 21 | PY | L |
| TILIACEAE | *Luehea seemannii* | 38 | 77 | PY | L |
| TILIACEAE | *Luehea speciosa* | 22 | 15 | PY | L |
| TILIACEAE | *Trichospermum galeottii* | 15 | 31 | PY | L |
| ARALIACEAE | *Dendropanax arboreus* | 44 | 21 | MD | V |
| MYRISTICEAE | *Virola surinamensis* | 45 | 24 | MD | L |
| MYRISTICACEAE | *Virola sebifera* | 12 | 84 | MPD | V |
| ANNONACEAE | *Annona spraguei* | 14.8 | 73 | MPD | L |
| ANNONACEAE | *Xylopia aromatica* | 9 | 83 | MPD | L |
| ANNONACEAE | *Xylopia frutescens* | 1.25 | 100 | MPD | L |
| ARALIACEAE | *Schefflera morototoni* | 65 | 35 | MPD | L |
| OLACACEAE | *Heisteria concinna* | 40 | 34 | MPD | S |
| RUBIACEAE | *Amaioua corymbosa* | 25 | 52 | MPD | V |

**Figure 16**. Number of species in each of the five dormancy classes. No species had combinational dormancy (PY=PD).

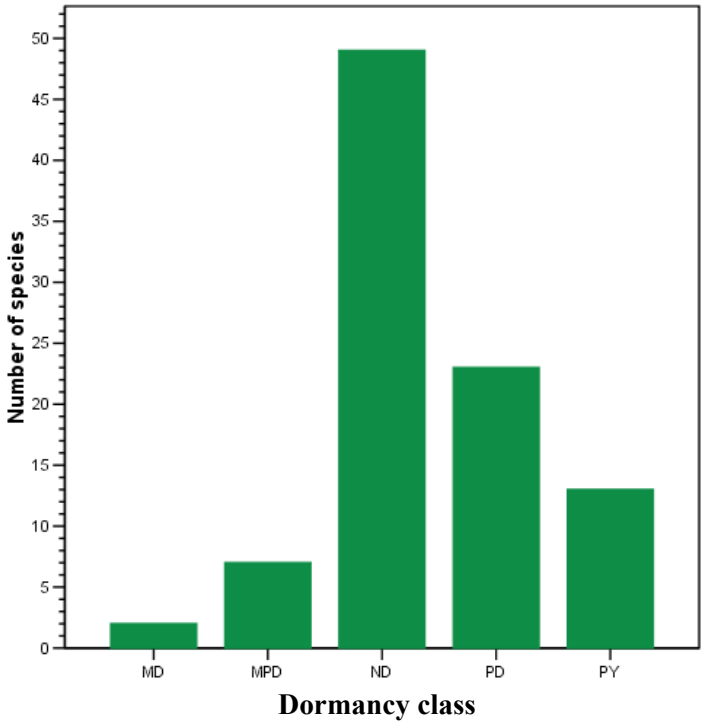



**Figure 17.** Time course for increase in mass of mechanically scarified and of non-scarified seeds of *Apeiba aspera* (Tiliaceae). Bars indicate ± SE. Seed initial MC was 8.79%.

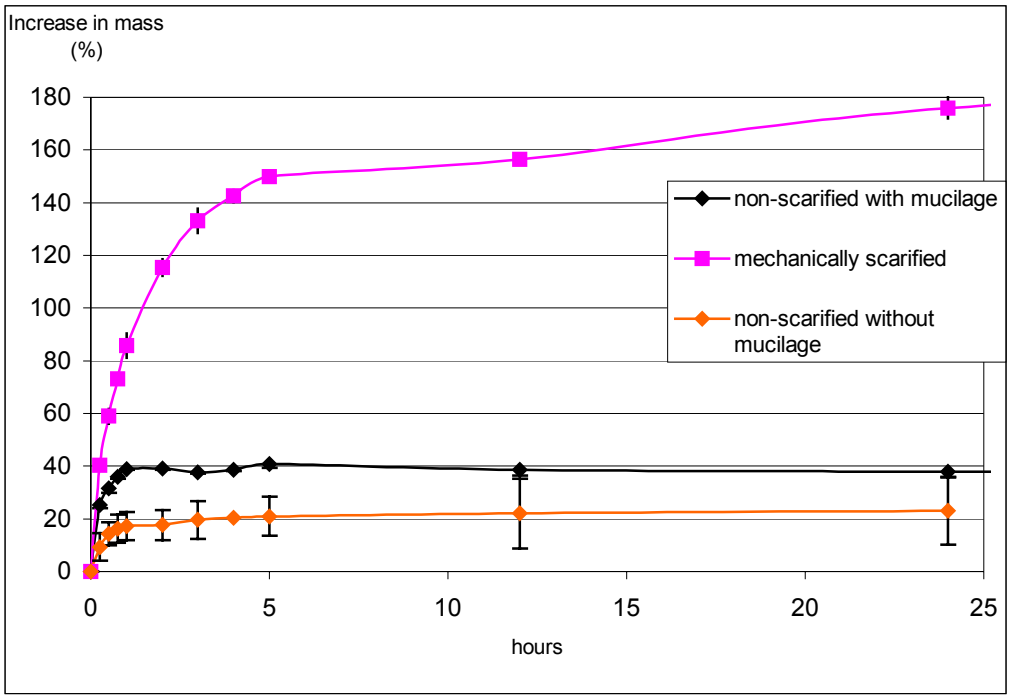


**Figure 18.** Time course for increase in mass of mechanically scarified, scarified in boiling water for 15 sec, and of non-scarified seeds of *Colubrina glandulosa* (Rhamaceae). Bars indicate ± SE. All seeds mechanically scarified rotted after 7 days. Seed initial MC was 12.06%.

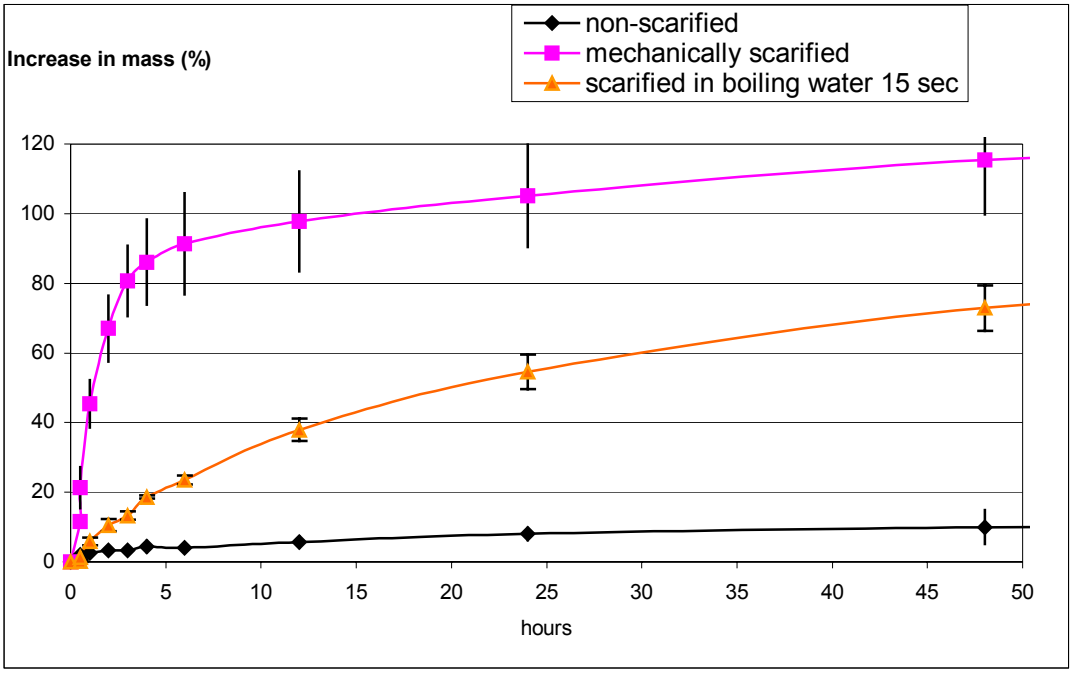



**Figure 19.** Time course for increase in mass of seeds of *Enterolobium cyclocarpum* (Fabaceae) mechanically scarified, scarified for 15 sec in boiling water, and non-scarified. Bars indicate ± SE. Arrow indicates radicle emergence. Initial seed MC was 21.03%.

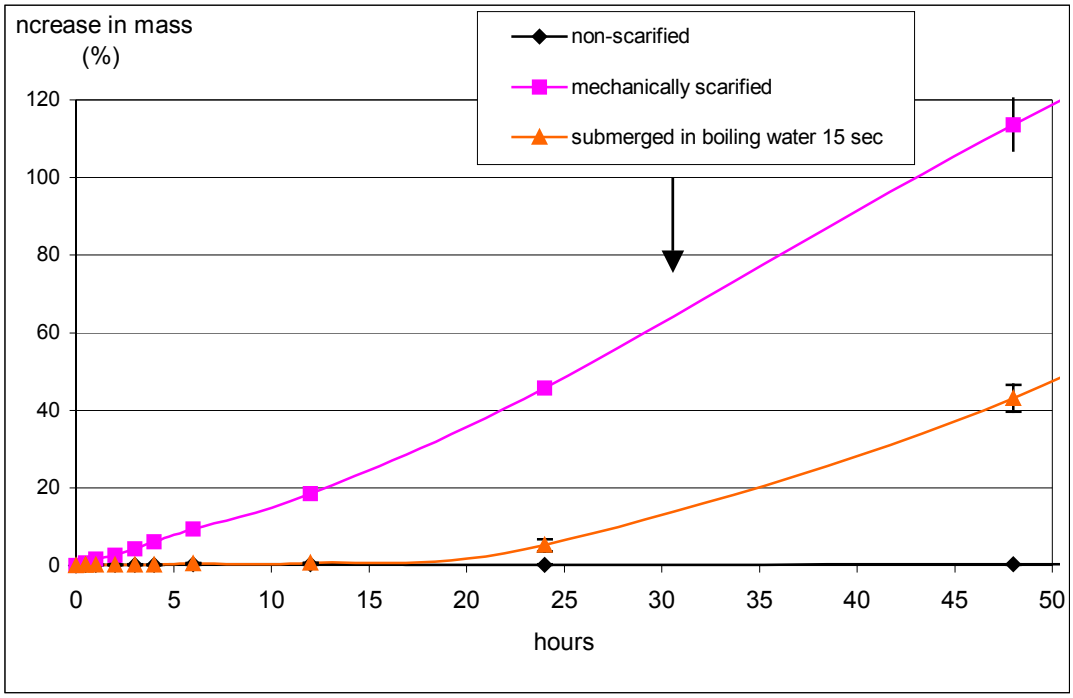


**Figure 20.** Time course for increase in mass of seeds of *Enterolobium schomburgkii* (Fabaceae) mechanically scarified, scarified for 15 sec in boiling water, and non-scarified. Bars indicate ± SE. Fifteen percent of non-scarified seeds imbibed. Seed initial MC was 28%.

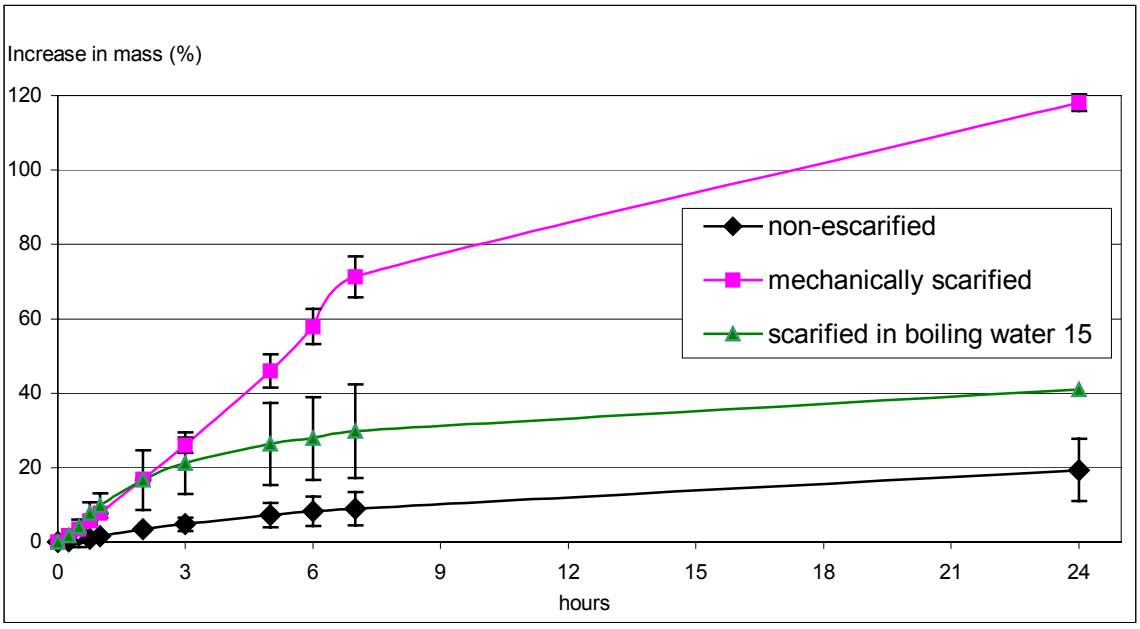



**Figure 21.** Time course for increase in mass of mechanically scarified and of non-scarified seeds of *Luehea seemannii* (Tiliaceae). Bars indicate ± SE. Initial MC was 11% (with wings).

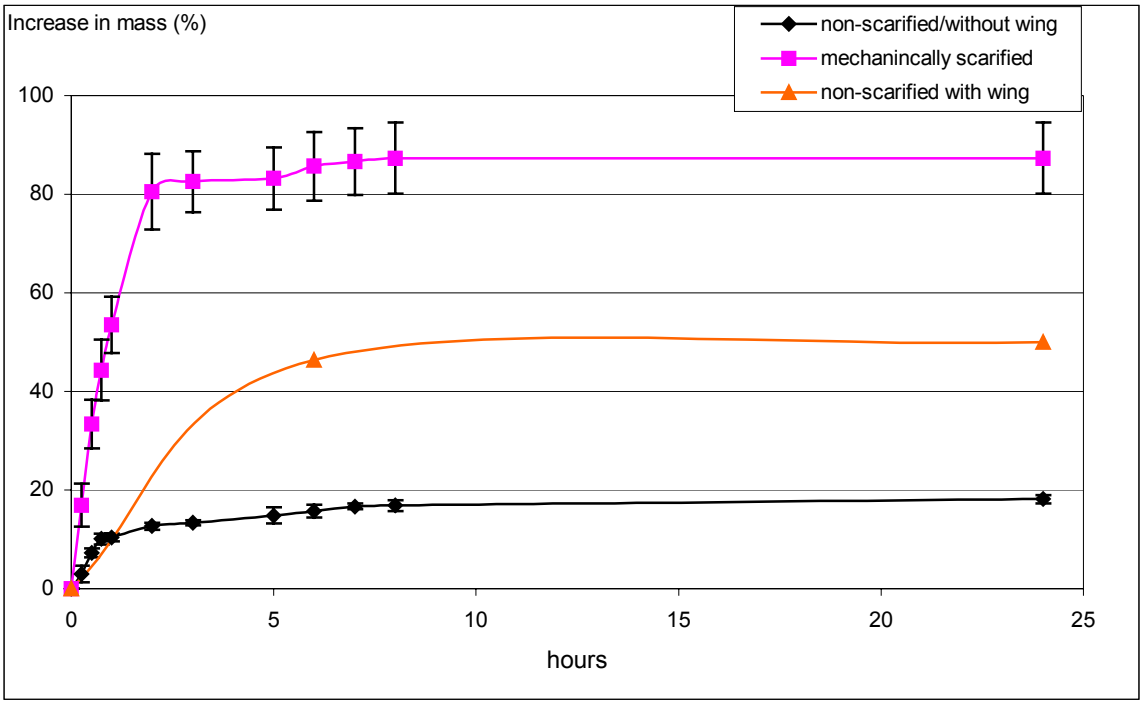


**Figure 22.** Time course for increase in mass of mechanically scarified and of non-scarified seeds of O*rmosia macrocalyx* (Fabaceae). Bars indicate ± SE. Seed initial MC was 13.5%.

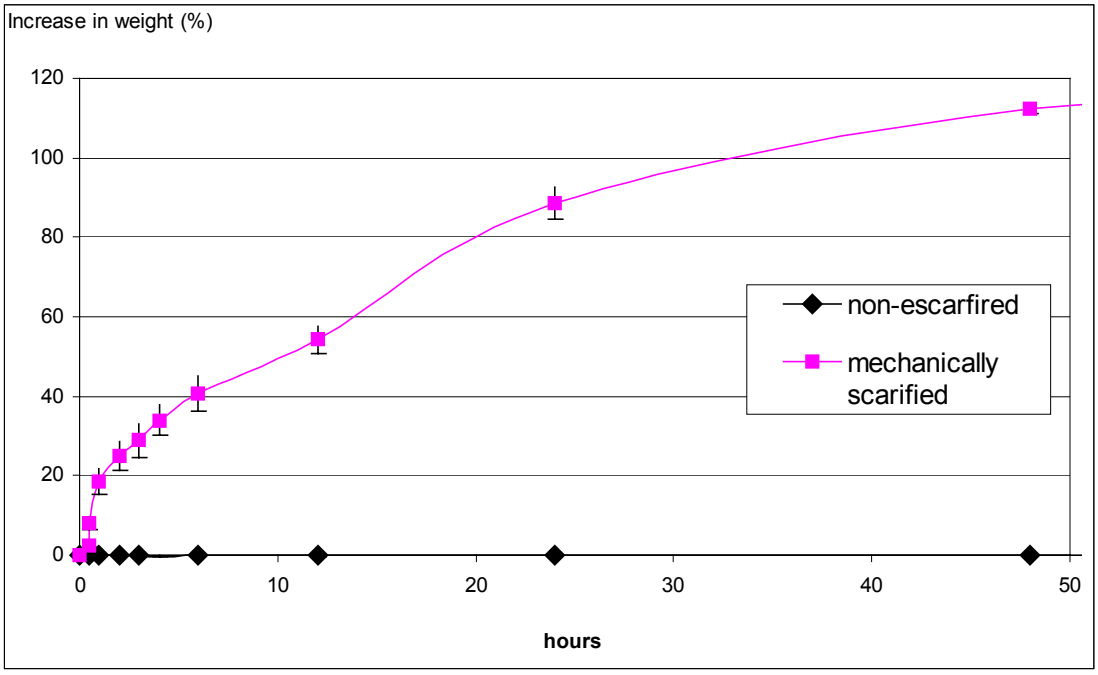



**Figure 23.** Time course for increase in mass of mechanically scarified and of non-scarified seeds of *Ficus insipida* (Moraceae). Bars indicate ± SE. Seeds become covered by mucilage, and half of the scarified ones geminated after 7 days. However, only 4 of 45 non-scarified seeds germinated. Seed initial MC was 12.2%.

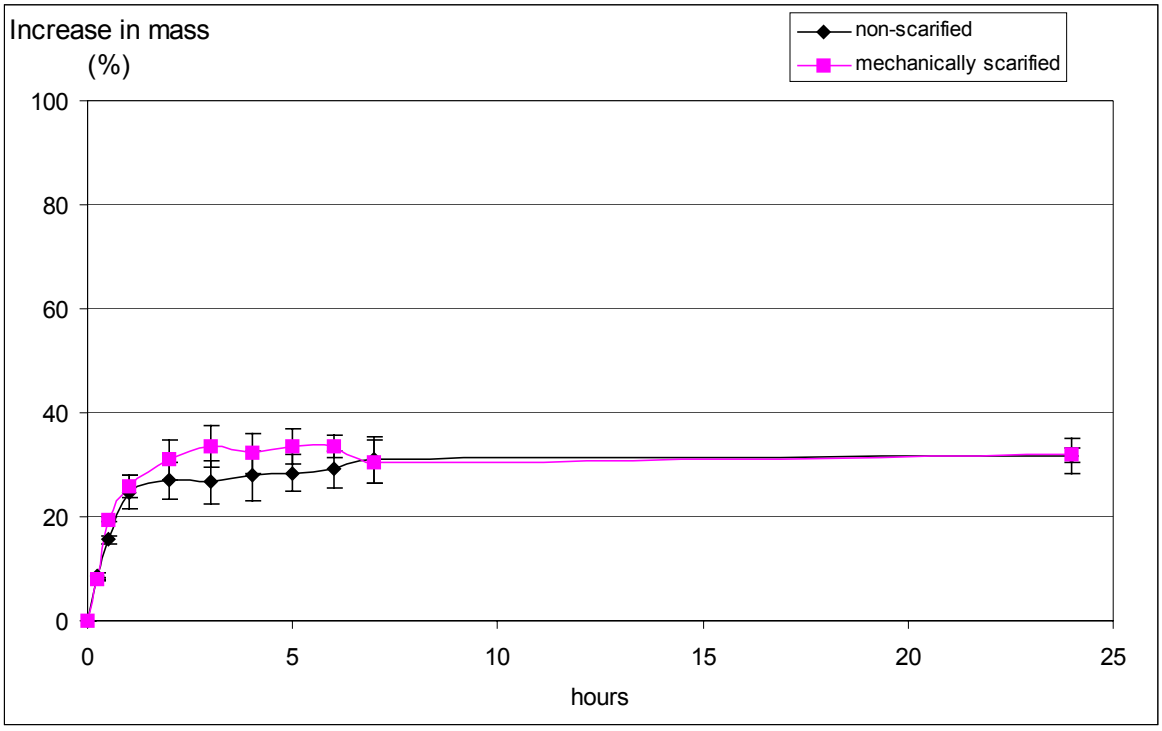


**Figure 24.** Time course for increase in mass of mechanically scarified and of non-scarified seeds of *Guarea guidonea* (Meliaceae). Bars indicate ± SE. Scarified seeds rotted after 10 days, and only 2 of 30 seeds germinated. Non-scarified seed did not germinate. Initial MC was 30.4%.

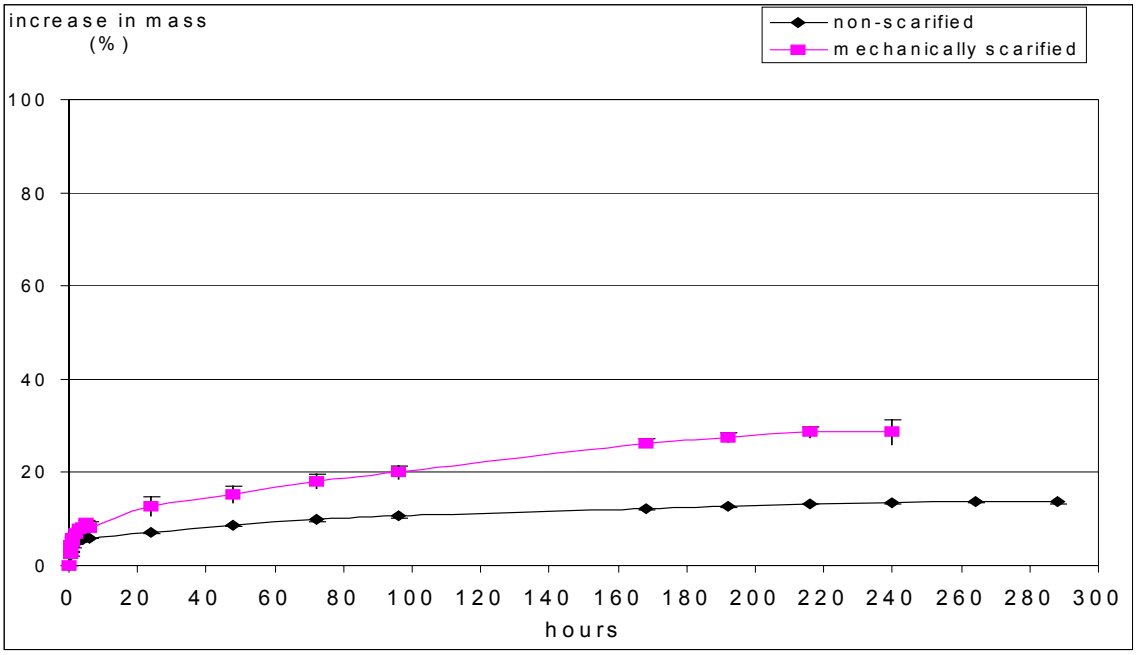



**Figure 25.** Time course for increase in mass of mechanically scarified and of non-scarified seeds of *Trema micrantha*. Bars indicate ± SE. Seed initial MC was 9.5%.

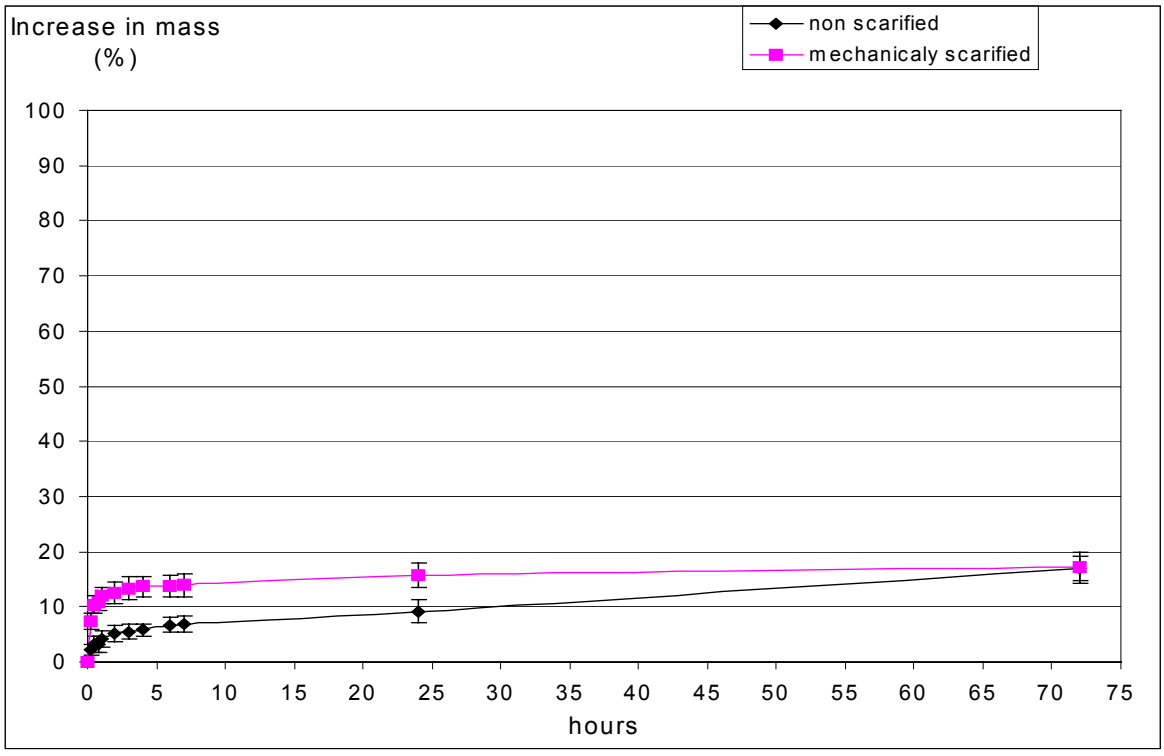


**Figure 26**. Time course for increase in mass of mechanically scarified and of non-scarified seeds of *Amaioua corymbosa* (Rubiaceae). Bars indicate ± SE. Seeds had an underdeveloped embryo and an oily and fibrous testa. Initial MC was 59.11%.

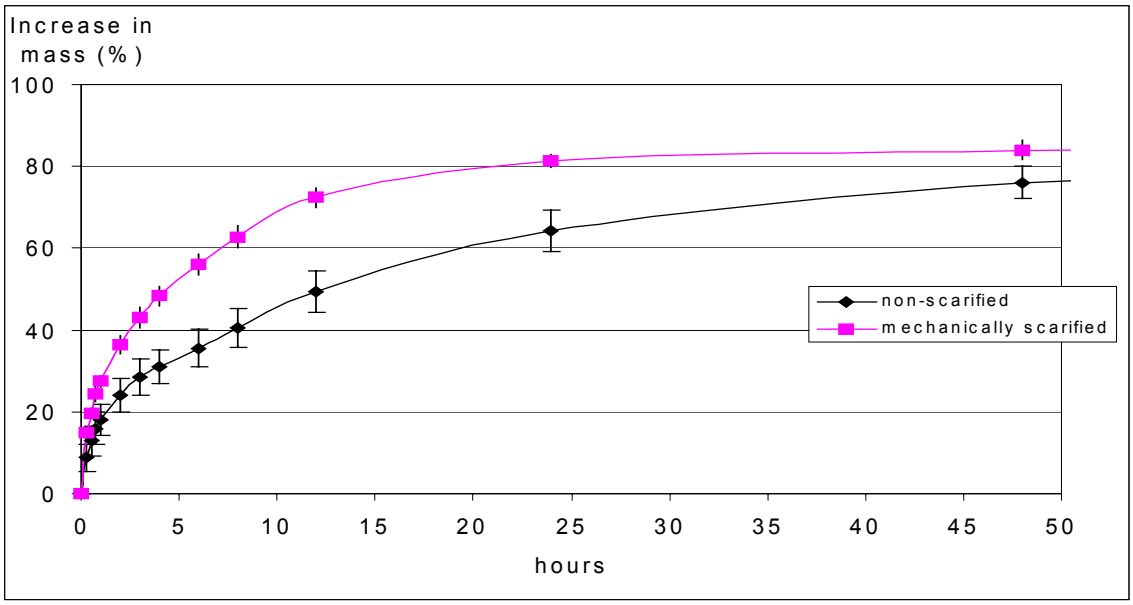



**Figure 27.** Time course for increase in mass of mechanically scarified and of non-scarified seeds of *Heisteria concinea* (Olacaceae). Bars indicate ± SE. Seeds have an underdeveloped embryo. Scarified seeds rotted after 7 days. Initial MC was 30%. .

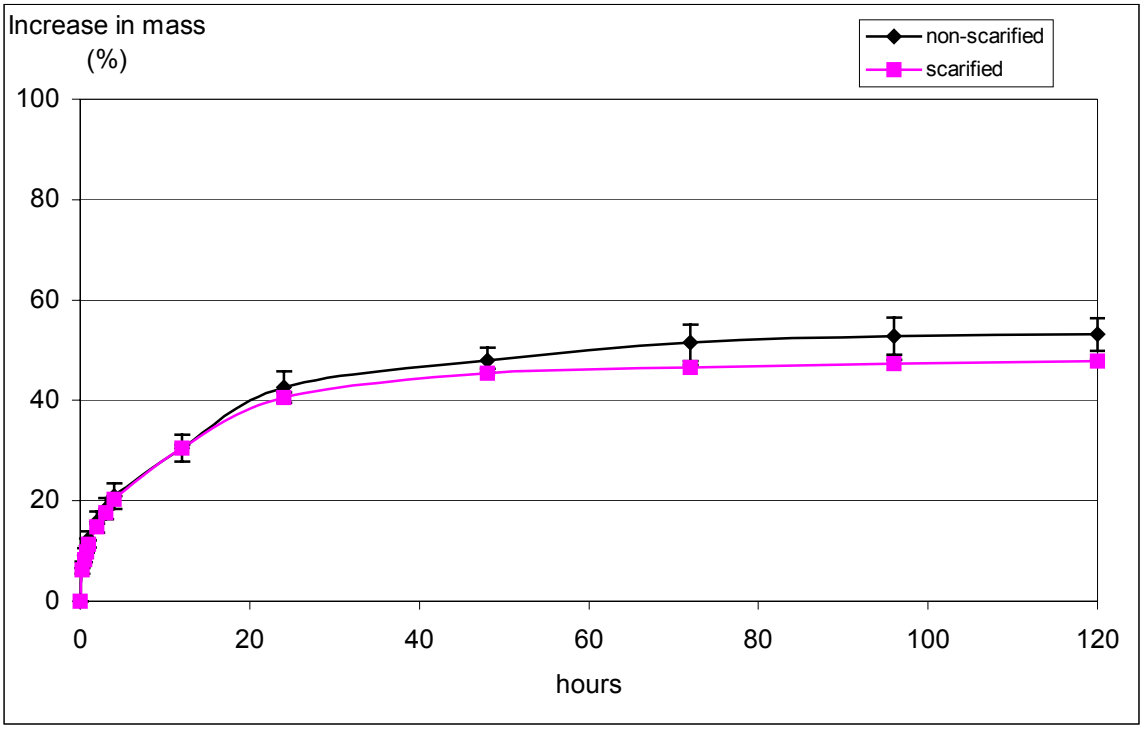


**Figure 28.** Time course for increase in mass of mechanically scarified and of non-scarified seeds of *Andira inermis* (Fabaceae). Bars indicate ± SE. Fifty percent of scarified seeds germinated after 10 days, and 4 of 30 non-scarified seeds germinated after 17 days. Seed initial MC was 57.2%.

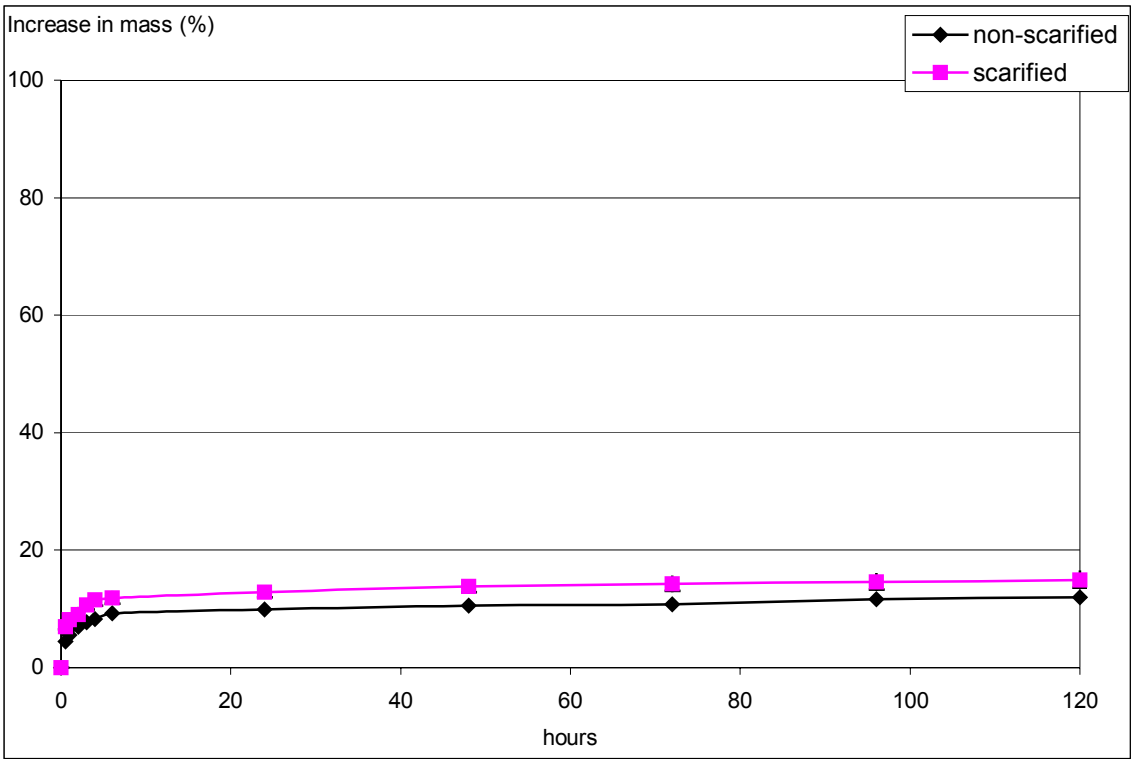


**Fig. 29.** Seeds of *Apeiba aspera* (Tiliaceae) after 72 hours of imbibition. M, Mucilage surrounded the seeds.

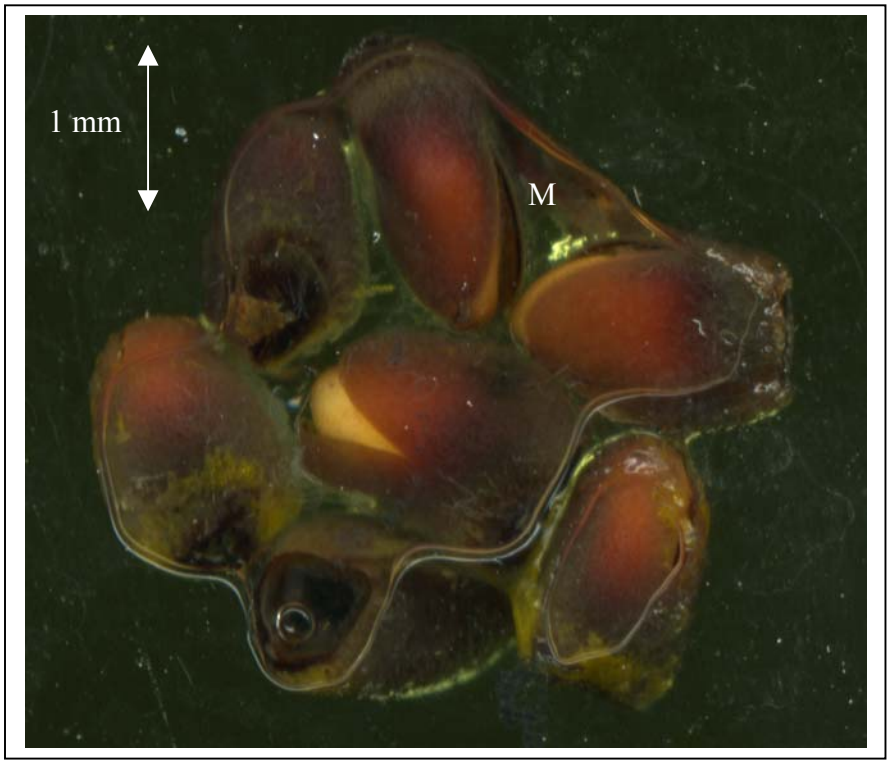


**Fig. 30.** Drawings of longitudinal sections of seeds with fully developed embryos. a, *Trema micrantha*; b, *Apeiba aspera*; c,*Guarea guidonea,* d*; Luehea seemannii*; e*, Trichilia hirta;* f, *Ficus insípida.* A, aril; C, cotyledon; E, endosperm; F, fruit wall; R, radicle; S, seed coat; W, wing.

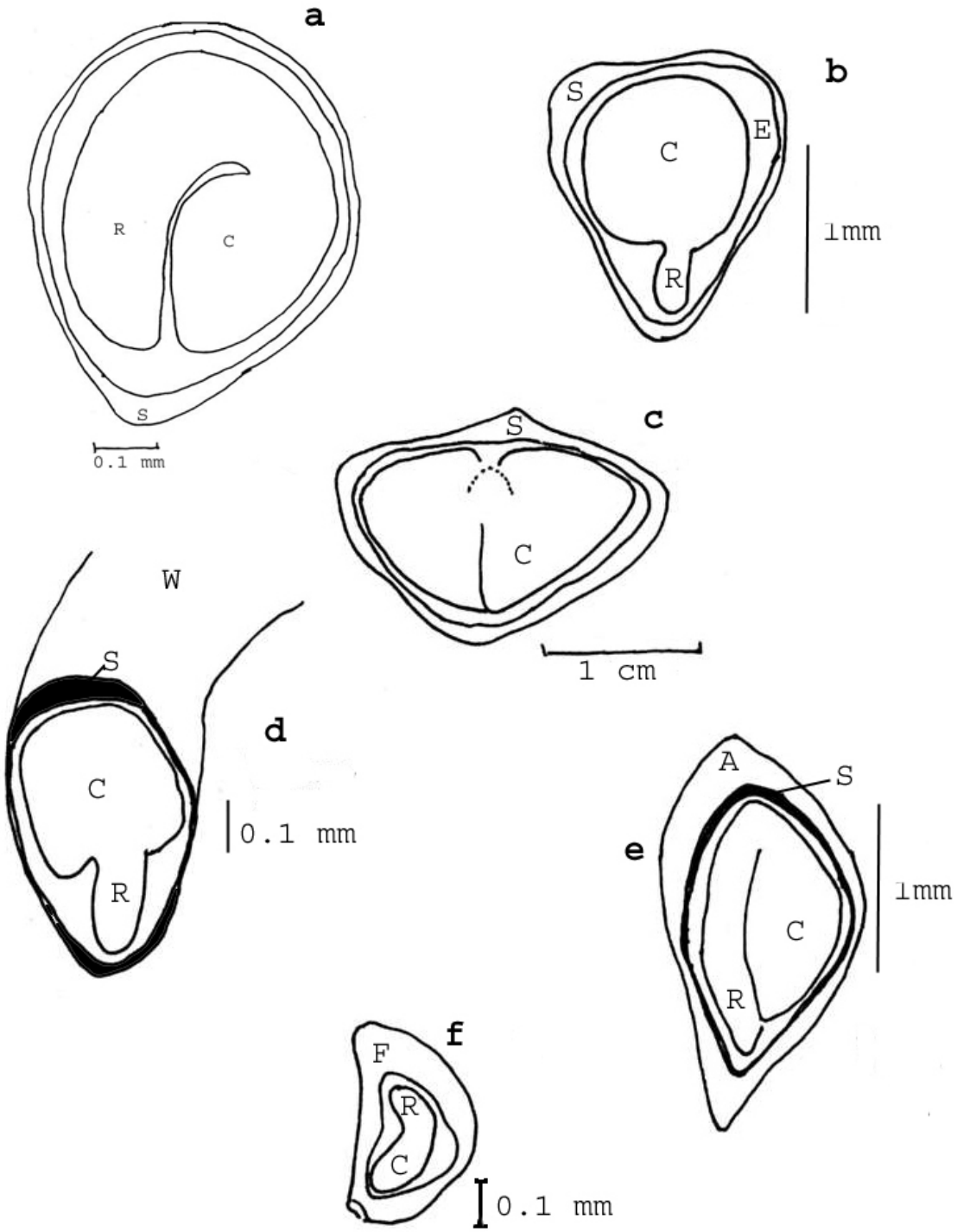


**Fig. 31.** Underdeveloped embryo of *Heisteria concinea* (Olacaceae). Seeds were imbibed for two days. C, cotyledon.

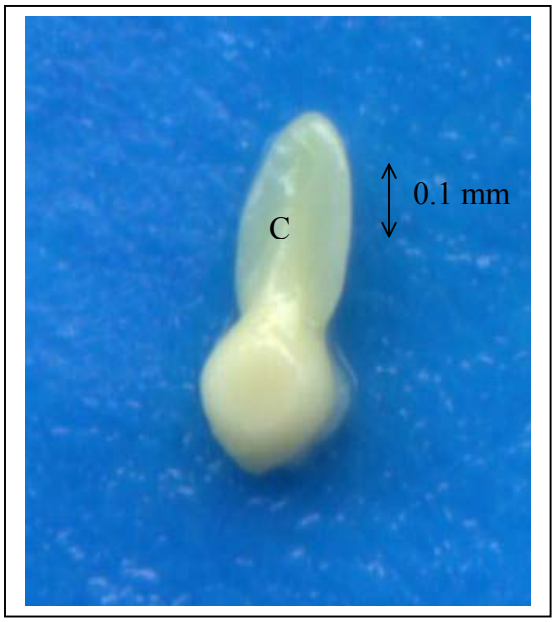



**Fig. 32.** Underdeveloped embryo of *Amaioia corymbosa* (Rubiaceae). C, cotyledon; R, radicle; E, endosperm; T, testa

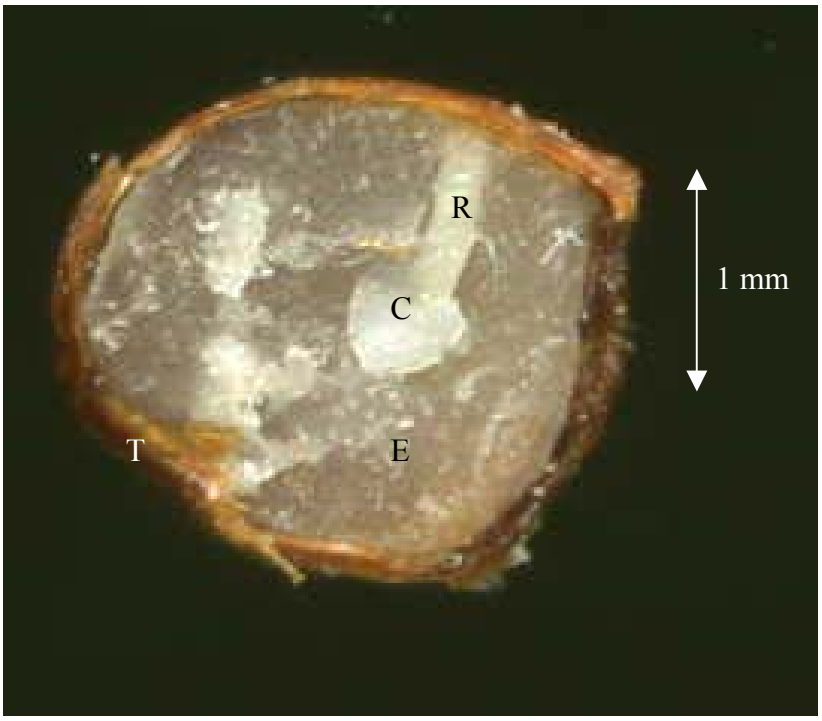


**Fig. 33**. Seed weight in each class of dormancy. MPD, morphological and morphophysiological dormancy (combined); ND, nondormant; PD, physiological dormancy; PY, physical dormancy. Letters represent subsets with significant differences. (Tukey HSD test, $p < 0.05$). See text for information on outliers and extremes.

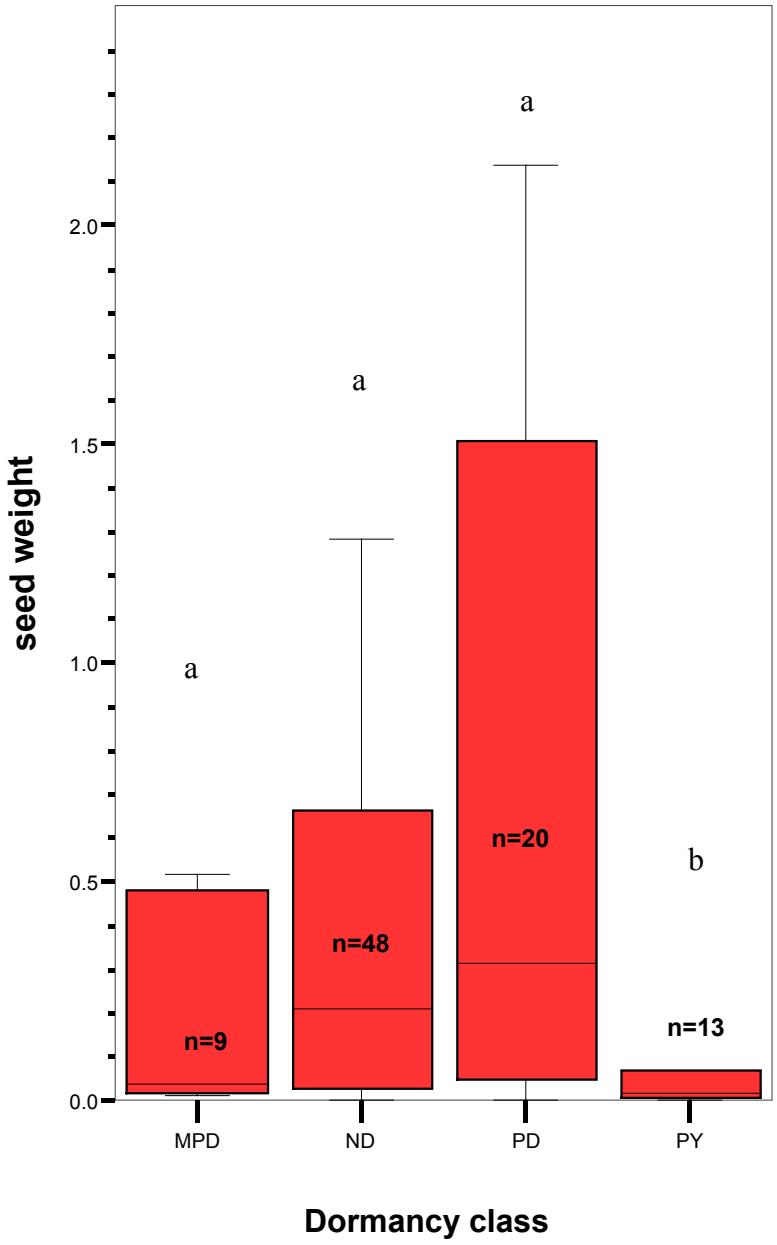


**Fig. 34.** Seed moisture content (MC) in each class of dormancy. MPD, morphological and morphophysiological dormancy (combined); ND, nondormant; PD, physiological dormancy; PY, physical dormancy. Circle represents an outlier. Letters represent subsets with significant differences.(Tukey HSD test, $p < 0.05$).

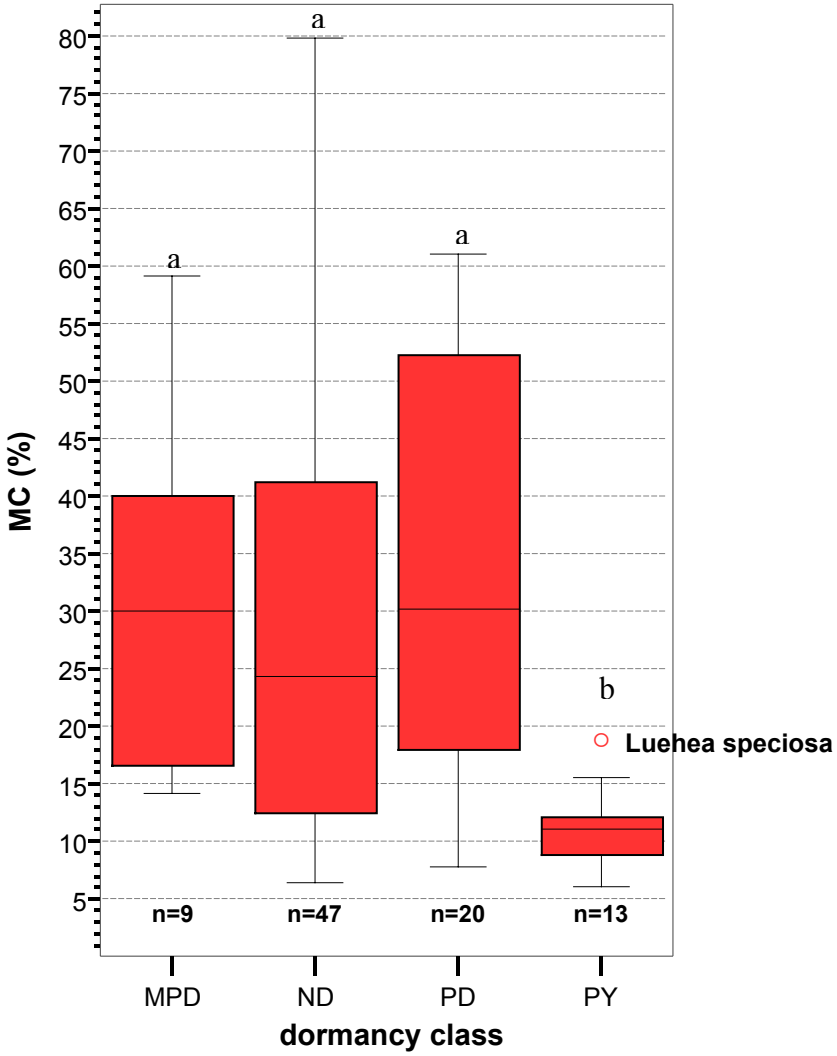


**Fig. 35**. Seed dispersal time of species within each class of dormancy. ND, non-dormant; PD, physiological dormancy; PY, physical dormancy; MPD, morphological and morphophysiological dormancy (combined). DS, dry season (January-April); ERS, early rainy season (May-August); LRS, late rainy season (September-December).

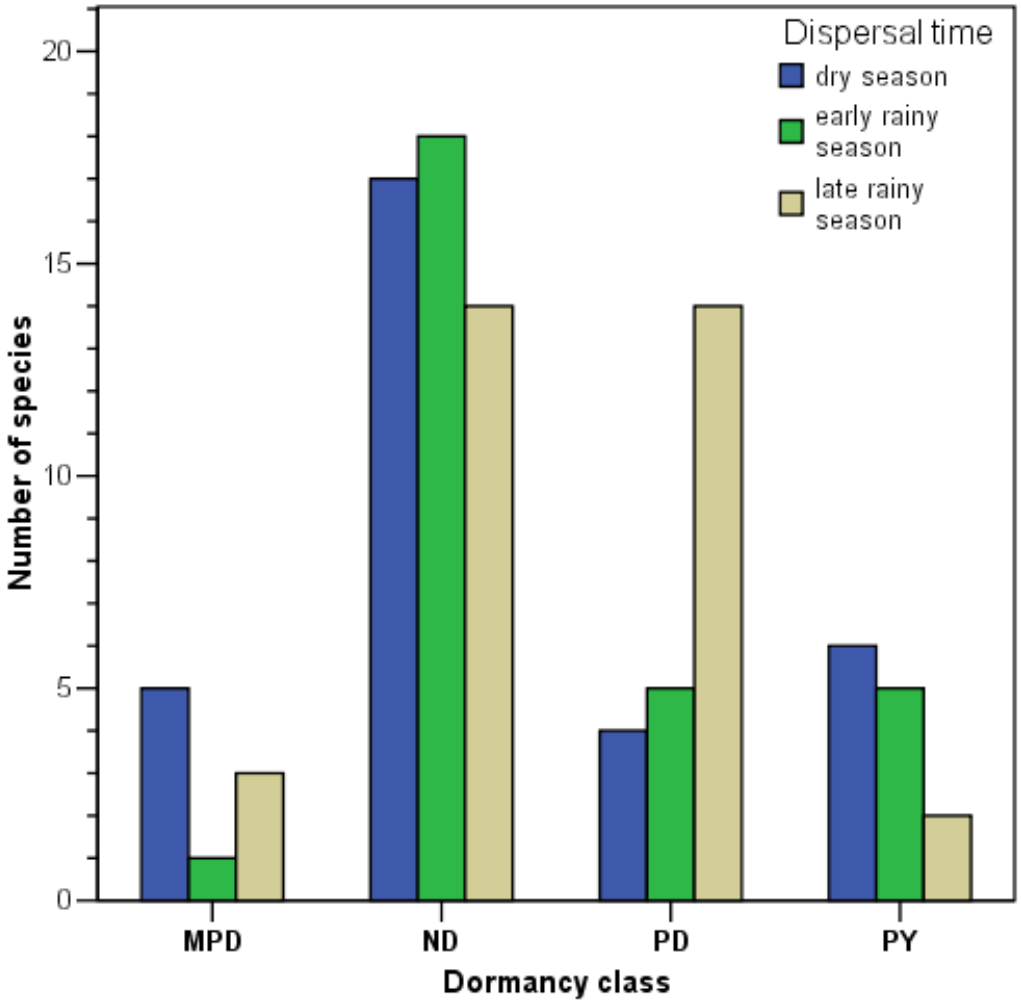


**Fig. 36**. Distribution of dormancy classes within successional categories of the study species.

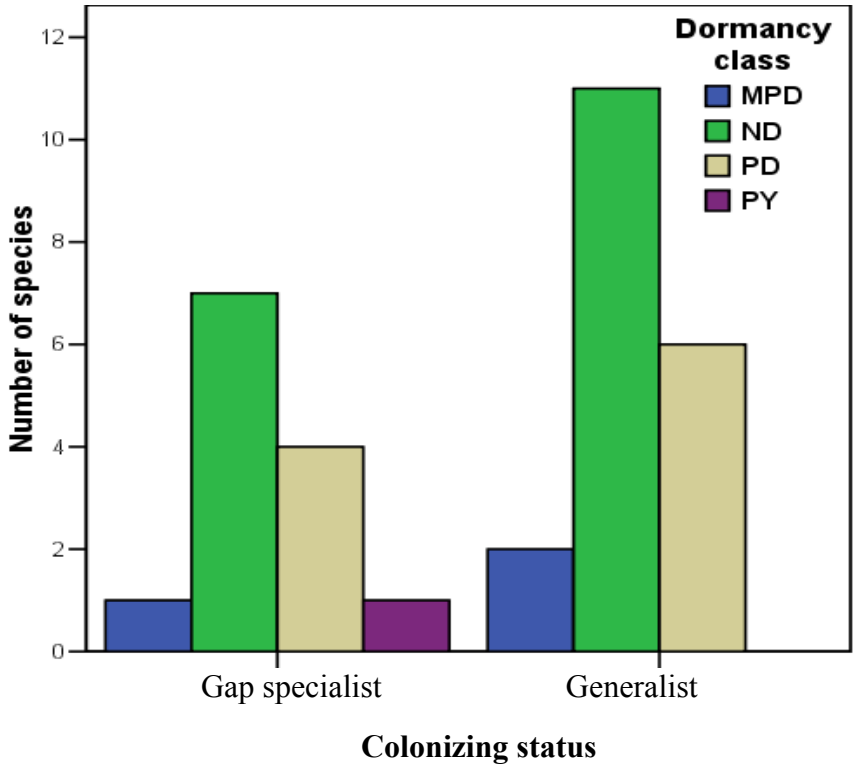



**Fig. 37.** Distribution of dormancy classes within growth-forms of the study species.

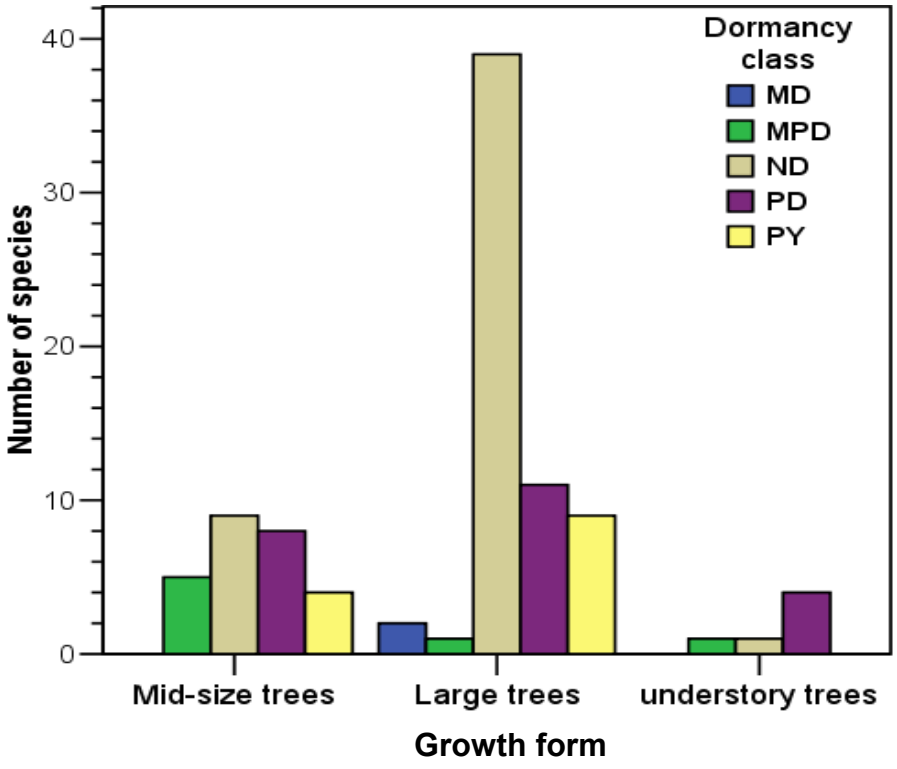
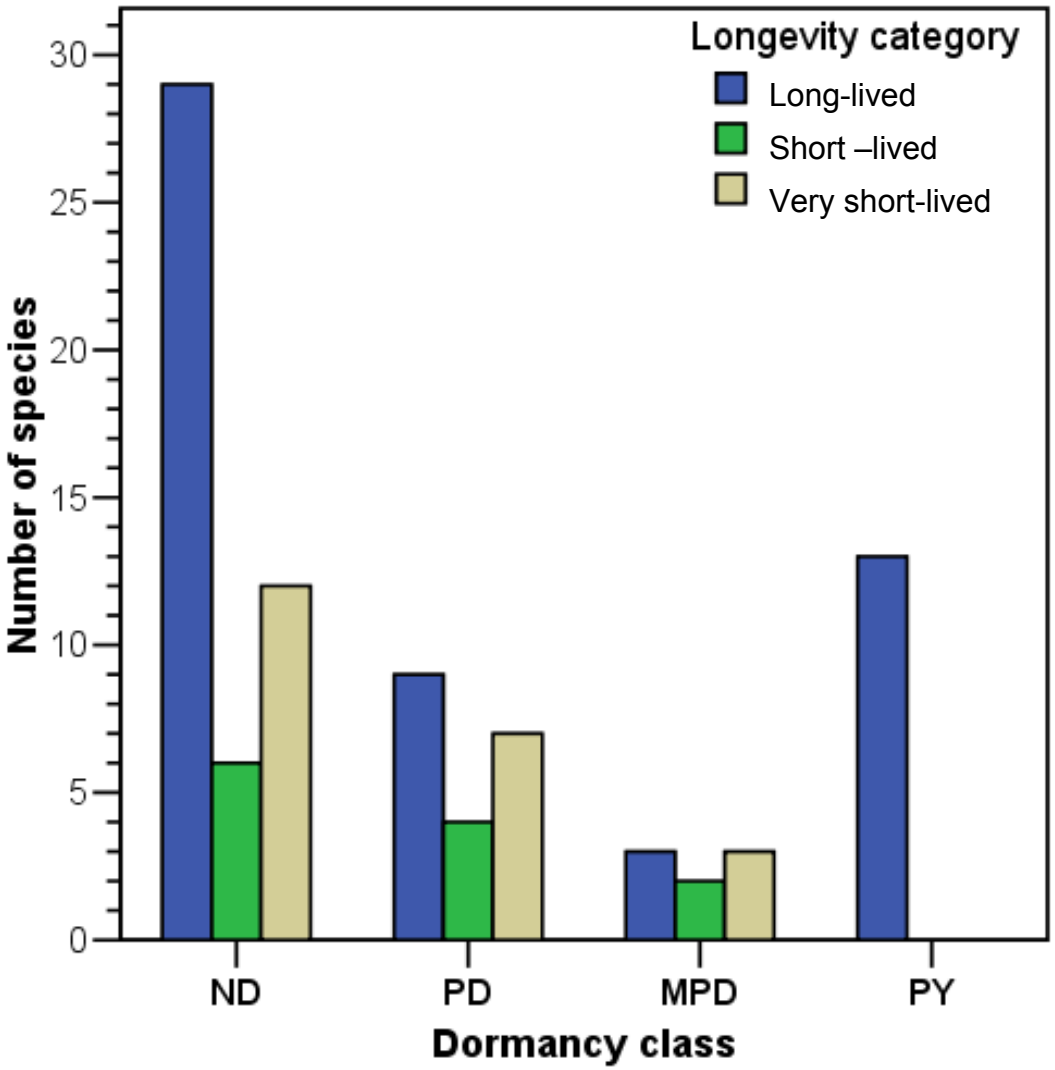


**Fig. 38.** Distribution of species in each class of dormancy within seed longevity categories. MPD, morphophysological and morphological dormancy (combined); ND, non-dormancy; PD, physiological dormancy; PY, physical dormancy. Seed storage behavior: V, very short lived (<1 month); S, short lived (1-4 months), L, long lived (>4 months, to decrease germination to < 5%).



## III. ANALYSIS OF DORMANCY AND SEED STORAGE BEHAVIOR ALONG THE RAINFALL GRADIENT

Ninety-two species whose dormancy class was established in this study were present in the set of 39 inventory plots that flanks the Panama Canal. Table 8 shows the distribution of species within the regions. The first region (1887-2124 mm of precipitation annually) had a total of 53 species present; the second (2125-2360 mm), 63; the third (2361-2598 mm), 76; the fourth (2599-2835 mm), 57; and the fifth (2836-3072 mm) 63. Tables 9 shows the proportion of species with seeds in each dormancy class for each region and Pearson correlation coefficients (r2) between classes of dormancy and mean annual precipitation (based in the mean precipitation for each region). For non-dormant (ND) species $r^2$= -0.75; physiologically dormant (PD), $r^2$= 0.56; physically dormant (PY), $r^2$= -0.92; morphologically dormant (MD), $r^2$= -0.32; and morphophysiologically dormant (MPD), $r^2$= -0.73. Proportions for each class of dormancy in each region are shown in Fig. 39. The proportion of species with ND and PD decreases with rainfall, that with PY and MPD increase, and that with MD is always very low. Fig. 40 shows the proportion of each class of dormancy within dormant species.

Based on longevity category I assigned to each species, I also calculated the proportion of species with long-lived seeds and of those with short + very short-lived seeds (combined) in each region (Tables 8, 9). The proportion of species with short + very short-lived seeds increases with rainfall (Pearson correlation coefficient=0.906) (Table 9, Fig. 41).

**Table 8.** Seed dormancy class, seed longevity category, and distribution of the study species through the rainfall gradient along the Panama Canal. Regions defined by mean annual precipitation. Seed dormancy class: ND, non-dormant; PD, physiological dormancy; PY, physical dormancy; MPD, morphophysiological dormancy; MD, morphological dormancy. Longevity category: V, very short-lived (<1 month); S, short-lived (1-4 months), L, long-lived (>4 months, to decrease germination to < 5%).

| Species | Seed dormancy class | Longevity category | 1887-2124 (mm) | 2135-2360 (mm) | 2361-2598 (mm) | 2598-2835 (mm) | 2835-3072 (mm) |
|---|---|---|---|---|---|---|---|
| ***Adelia triloba*** | ND | L | X | X | X | | X |
| ***Albizia adinocephala*** | ND | L | X | | | | |
| ***Alseis blackiana*** | ND | L | X | X | X | X | |
| ***Amaioua corymbosa*** | MPD | V | X | X | X | X | X |
| ***Anacardium excelsum*** | ND | S | X | X | X | X | X |
| ***Andira inermis*** | PD | V | X | X | X | X | X |
| ***Annona spraguei*** | MPD | L | X | X | X | X | X |
| ***Antirhea trichantha*** | PD | L | X | X | X | X | |
| ***Apeiba aspera*** | PY | L | | X | X | X | X |
| ***Apeiba tibourbou*** | PY | L | | | X | X | X |
| ***Aspidosperma cruentum*** | ND | V | | X | X | X | X |
| ***Beilschmiedia pendula*** | ND | ---- | | | X | X | X |
| ***Brosimum utile*** | ND | S | | | | | X |
| ***Bursera simaruba*** | ND | L | X | X | X | | X |
| ***Byrsonima crassifolia*** | PD | L | | X | X | | |
| ***Calophyllum longifolium*** | ND | V | | X | X | X | X |
| ***Calycophyllum candidissimum*** | ND | L | X | X | X | | X |
| ***Carapa guianensis*** | ND | V | | | | | X |
| ***Castilla elastica*** | ND | V | | X | | X | |
| ***Cedrela odorata*** | ND | L | X | | | | |
| ***Ceiba pentandra*** | ND | L | | | X | | X |
| ***Chrysophyllum cainito*** | ND | L | X | X | X | | X |
| ***Colubrina glandulosa*** | PY | L | X | | X | X | |
| ***Copaifera aromatica*** | ND | L | X | | X | | |
| ***Cordia alliodora*** | ND | L | X | X | X | X | X |
| ***Cupania latifolia*** | PD | V | | X | X | | X |
| ***Dalbergia retusa*** | ND | L | X | | X | | |
| ***Dendropanax arboreus*** | MD | V | X | X | X | X | X |
| ***Dialium guianense*** | PY | L | | X | | | |
| ***Diphysa robinioides*** | ND | L | X | | | | |
| ***Dipteryx panamensis*** | PD | V | | X | X | | |
| ***Enterolobium cyclocarpum*** | PY | L | | | X | | |
| ***Enterolobium schomburgkii*** | PY | L | | X | X | | |
| ***Faramea occidentalis*** | PD | V | X | X | X | X | X |
| ***Ficus insipida*** | ND | L | X | X | X | X | X |
| ***Genipa americana*** | ND | S | X | X | | | |

**Table 8** (continued)

| Species | Seed dormancy class | Longevity category | 1887-2124 (mm) | 2135-2360 (mm) | 2361-2598 (mm) | 2598-2835 (mm) | 2835-3072 (mm) |
|---|---|---|---|---|---|---|---|
| ***Guarea grandifolia*** | PD* | V* | X | X | X | X | X |
| ***Guarea guidonia*** | PD | V | X | X | X | X | X |
| ***Guazuma ulmifolia*** | PY | L | X | X | X | X | X |
| ***Guettarda foliacea*** | PD | ---- | | | X | X | X |
| ***Gustavia superba*** | PD | S | | X | X | X | X |
| ***Hampea appendiculata*** | ND | S | | | | X | X |
| ***Hasseltia floribunda*** | ND | V | | X | X | X | |
| ***Heisteria concinna*** | MPD | S | X | X | X | X | X |
| ***Hura crepitans*** | ND | L | | X | X | X | X |
| ***Hyeronima alchorneoides*** | PD | S | | | X | X | X |
| ***Hymenaea courbaril*** | ND | S | X | | X | X | |
| ***Inga punctata*** | ND | V | X | | | | |
| ***Inga spectabilis*** | ND | V | | X | X | | X |
| ***Jacaranda copaia*** | ND | L | X | X | X | X | X |
| ***Lacmellea panamensis*** | ND | V | | X | X | X | X |
| ***Lafoensia punicifolia*** | ND | L | | X | | | |
| ***Lindackeria laurina*** | PD | V | X | X | X | X | |
| ***Lonchocarpus latifolius*** | ND | L | X | | X | X | X |
| ***Luehea seemannii*** | PY | L | X | X | X | X | X |
| ***Luehea speciosa*** | PY | L | X | | | | |
| ***Margaritaria nobilis*** | PD | ---- | | X | X | | X |
| ***Miconia argentea*** | ND | L | | | X | X | X |
| ***Miconia minutiflora*** | PD | L | | X | X | X | X |
| ***Ochroma pyramidale*** | PY | L | X | | | | |
| ***Ormosia macrocalyx*** | PY | L | X | X | X | | X |
| ***Pachira quinata*** | ND | L | X | X | X | | X |
| ***Phoebe cinnamomifolia*** | ND | V | X | X | X | X | X |
| ***Posoqueria latifolia*** | PD | S | X | | X | X | X |
| ***Prioria copaifera*** | PD | S | | | X | | X |
| ***Protium panamense*** | ND | ---- | | X | X | X | X |
| ***Protium tenuifolium*** | ND | S | X | X | X | X | X |
| ***Pseudobombax septenatum*** | ND | L | X | X | X | | X |
| ***Pseudosamanea guachapele*** | PY | L | X | | | | |
| ***Pterocarpus rohrii*** | ND | L | | X | X | X | X |
| ***Quararibea asterolepis*** | ND | V | | | X | X | X |
| ***Sapindus saponaria*** | PD | L | X | X | | | |
| ***Sapium glandulosum*** | PD | L | X | X | X | X | X |
| ***Schefflera morototoni*** | MPD | S | X | X | X | X | X |
| ***Spondias mombin*** | PD | L | X | X | X | X | X |
| ***Spondias radlkoferi*** | PD | L | X | X | X | X | X |
| ***Sterculia apetala*** | ND | L | X | | X | X | |
| ***Swietenia macrophylla*** | ND | L | X | X | | | |
| ***Tabebuia guayacan*** | ND | L | | X | X | X | X |

**Table 8** (continued)

| Species | Seed dormancy class | Longevity category | 1887-2124 (mm) | 2135-2360 (mm) | 2361-2598 (mm) | 2598-2835 (mm) | 2835-3072 (mm) |
|---|---|---|---|---|---|---|---|
| ***Tabebuia rosea*** | ND | L | X | X | X | X | X |
| ***Tachigalia versicolor*** | PD | S | | X | X | X | X |
| ***Tapirira guianensis*** | ND | V | | X | X | X | X |
| ***Trattinnickia aspera*** | ND | ---- | | | X | X | X |
| ***Trema micrantha*** | PD | L | | | X | | |
| ***Trichilia hirta*** | ND | L | X | X | X | | |
| ***Trichilia tuberculata*** | ND | V | X | X | X | X | X |
| ***Trichospermum galleottii*** | PY | L | X | X | X | | X |
| ***Vantanea depleta*** | PD | L | | X | X | X | X |
| ***Virola sebifera*** | MPD | V | X | X | X | X | X |
| ***Virola surinamensis*** | MD | L | | | X | X | X |
| ***Vochysia ferruginea*** | ND | L | | X | X | X | X |
| ***Xylopia frutescens*** | MPD | --- | X | X | X | X | |
| **TOTAL # SPECIES** | 92 | 89 | 53 | 63 | 76 | 57 | 63 |

**Table 9.** Proportions of species with seeds in each dormancy class and seed longevity category. Regions are defined by mean annual precipitation. Dormancy classes: ND, non-dormant; PD, physiological dormancy; PY, physical dormancy; MPD, morphophysiological dormancy; MD, morphological dormancy. Longevity categories: V, very short lived (<1 month); S, short lived (1-4 months), L, long lived (>4 months, to decrease germination to < 5%).

| | 1887-2124 (mm) | 2135-2360 (mm) | 2361-2598 (mm) | 2598-2835 (mm) | 2835-3072 (mm) | Pearson Correlation Coefficient |
|---|---|---|---|---|---|---|
| **Proportion of dormancy classes within all species** | | | | | | |
| ND | 52.8 | 50.8 | 51.3 | 54.4 | 57.1 | 0.75 |
| PD | 20.8 | 28.6 | 28.9 | 28.1 | 27.0 | 0.56 |
| PY | 15.1 | 11.1 | 10.5 | 7.0 | 7.9 | -0.92 |
| MD | 1.9 | 1.6 | 1.3 | 1.8 | 1.6 | -0.32 |
| MPD | 9.4 | 7.9 | 7.9 | 8.8 | 6.3 | -0.73 |
| **Proportion of dormancy classes within species with dormant seeds** | | | | | | |
| PD | 44 | 58 | 59 | 62 | 63 | 0.86 |
| PY | 32 | 23 | 22 | 15 | 19 | -0.86 |
| MD | 4 | 3 | 3 | 4 | 4 | 0.01 |
| MPD | 20 | 16 | 16 | 19 | 15 | -0.52 |
| | | | | | | |
| **Longevity categories proportions** | | | | | | |
| Long-lived | 71 | 63 | 65 | 58 | 58 | -0.906 |
| Short-lived + Very short-lived | 29 | 37 | 35 | 42 | 42 | 0.906 |

**Fig. 39.** Distribution of the proportions of species with seeds in each dormancy class through the rainfall gradient along the Panama Canal. Regions are defined by average mean annual precipitation. Seed dormancy class: ND, non-dormant; PD, physiological dormancy; PY, physical dormancy; MPD, morphophysiological dormancy; MD, morphological dormancy.

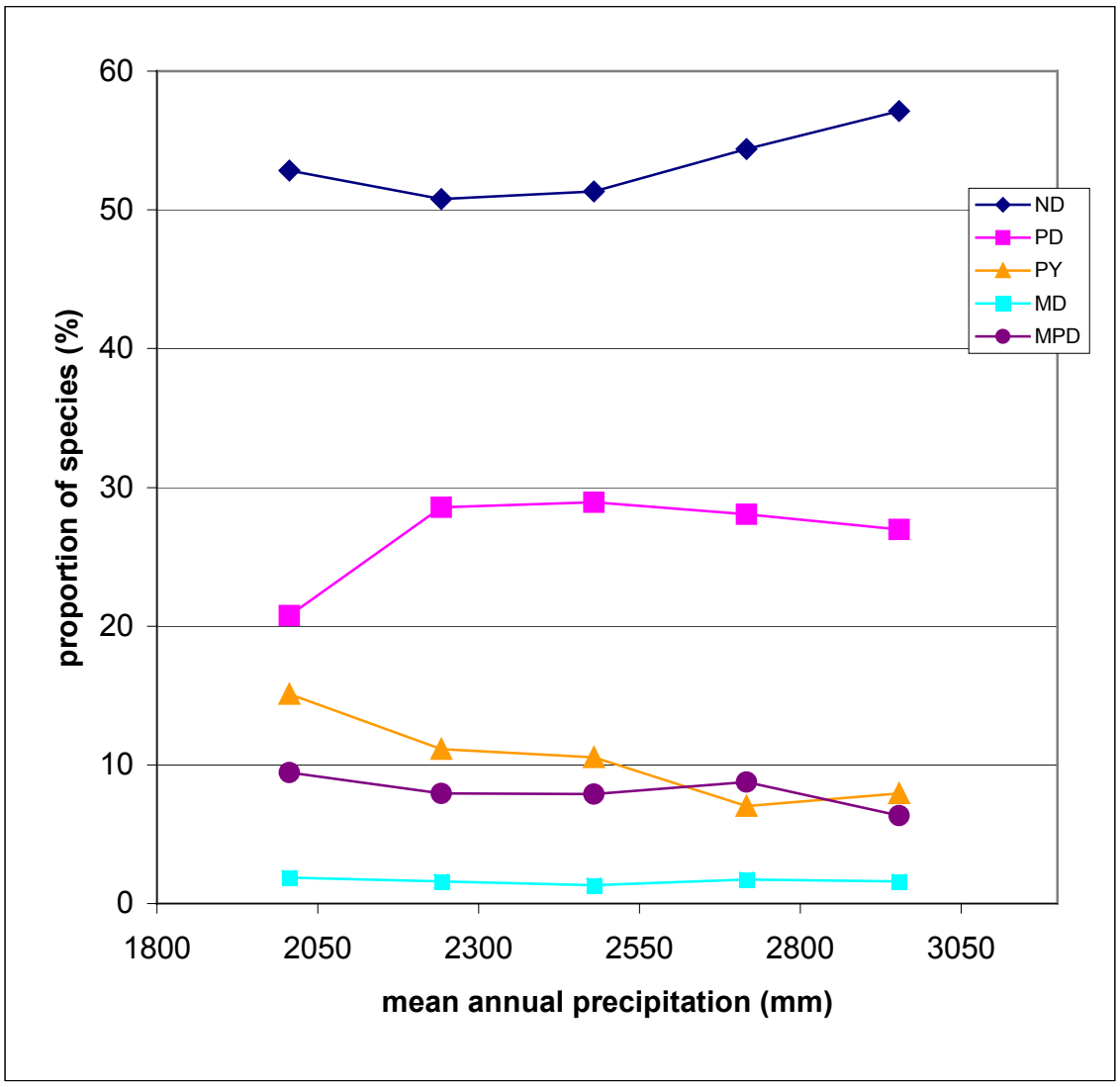


**Fig. 40.** Distribution of the proportions of species with seeds in each of four dormancy classes (within species with dormant seeds) through the rainfall gradient along the Panama Canal watershed. Regions are defined by average mean annual precipitation. Seed dormancy class: PD, physiological dormancy; PY, physical dormancy; MPD, morphophysiological dormancy; MD, morphological dormancy.

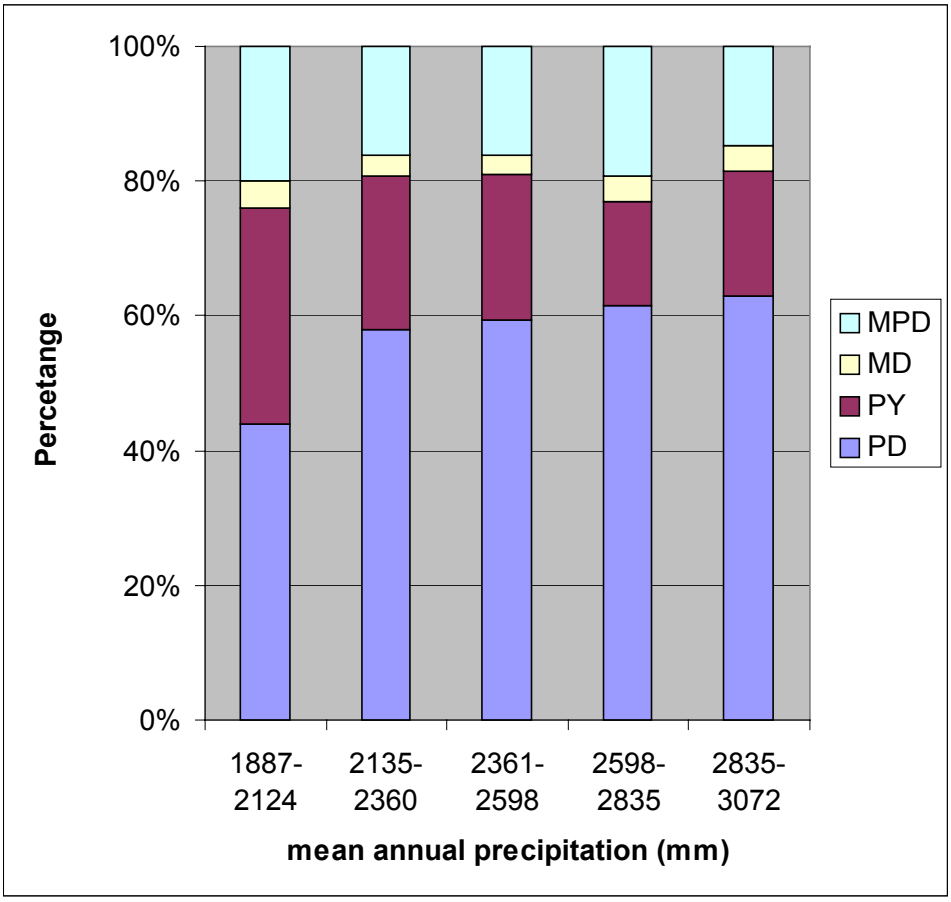
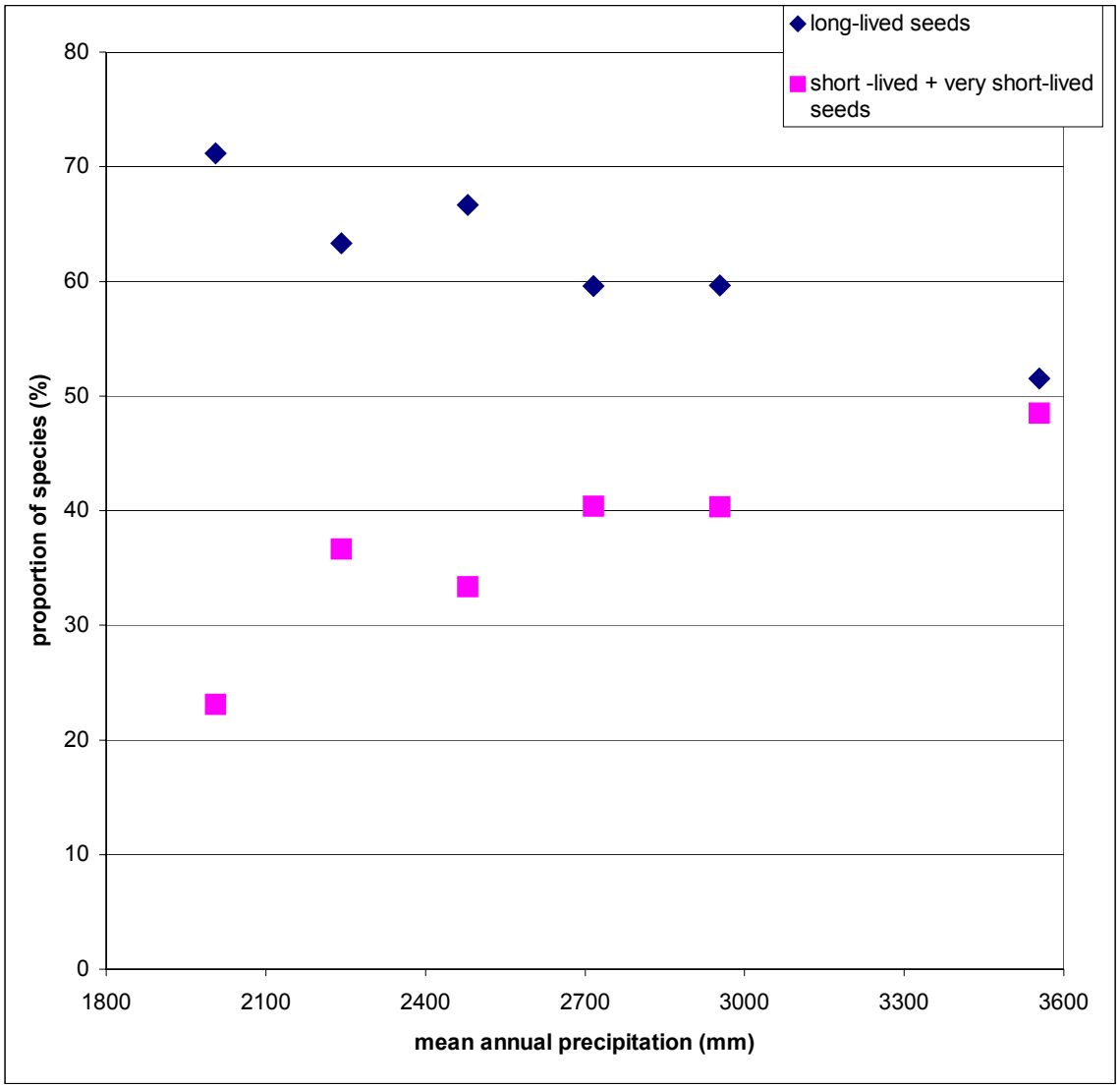


**Fig. 41.** Distribution of the proportions of species with seeds in each category of seed longevity through the rainfall gradient along the Panama Canal. Regions are defined by average mean annual precipitation. Longevity categories: very short-lived (<1 month); short-lived (1-4 months), long-lived (>4 months, to decrease germination to < 5%).



# DISCUSSION

## Germination data at the species level

There are few reports on seed germination of most of my study species and even fewer for Panamanian populations of them (Acuña and Garwood, 1987; Augspurger, 1986; Garwood, 1986a; Garwood, 1986b; Garwood and Lighton, 1990; Ibáñez et al., 1999; Kitajima and Augspurger, 1989; Sork, 1985). For 22 of the 94 species for which I have germination data, there is no previous information related to seeds and germination at the species level, and for 19 species the only information of this kind is that of Garwood (1983). No data are available for *Adelia triloba, Albizia adinocephala, Amaioua corymbosa, Antirrhea trichanta, Aspidosperma cruenta, Beilshmiedia pendula, Brosimun utile, Copaifera aromatica, Cupania latifolia, Dialium guianense, Erythrina fusca, Guetarda foliacea, Inga spectabilis, Lonchocarpus latifolius, Luehea speciosa, Miconia argentea, M. minutiflora, Phoebe cinnamomifolia, Protium panamense, Trattinnickia aspera, Trichilia tuberculata,* or *Xylopia aromatica*.

Some of the germination data presented by Garwood (1983) were obtained with very few seeds, and in many cases replicates were sown in different months of the year. Mean length of germination between replicates varied enormously in some species. Seeds were subjected to environmental differences throughout maturation, increasing chances for different germination responses due to preconditioning in seeds (Baskin and Baskin, 1998). My classification of dormancy class for *Calophyllum longifolium, Posoqueria latifolia*, and *Virola surinamensis* agrees with only one of the time-replicates in Garwood's data. Seeds of *Prioria copaifera*, collected from the soil in both studies, are less dormant in my experiments for seeds sown in July (Mean LG=32.9 days), than reported by Garwood (1983) for seeds sown in April (Mean LG= 64 days). The unknown time these seeds had been on the soil, as well as seasonal and annual climate variations, might explain some of the differences.

Garwood's (1983) data support my classification of dormant seeds for *Annona spraguei, Faramea occidentalis, Ficus insipida, Heisteria concinna, Lindackeria laurina, Margaritaria nobilis, Sapium glandulosum, Spondias mombin, Spondias raldkoferii, Trema micrantha, Vantanea depleta, Virola sebifera*, and *Xylopia frutescens;* and of nondormant seeds for *Hampea appendiculata, Hasseltia floribunda, Protium tenuifolium, Pterocarpus rorhii, Quararibea asterolpis,* and *Tabebuia guayacan*.

Classification as nondormant for seeds of *Castilla elastica* is supported by data of González (1991) and for *Tapirira guianense* and *Trichilia hirta* by data of Lorenzi (1992). Data in Gelfius (1994) and Vega et al. (1983) support the classification as dormant for seeds of *Byrsonima crassifolia.*

I suggest that differences between values reported here and those in other studies might be related to differences in initial seed moisture content (MC), but MC has been reported for seeds of only a few species. Collection methods and manipulation of seeds between field and nursery or laboratory, selection of well-formed seeds, and laboratory procedures also might explain some of the differences. Seeds of *Dendropanax arboreus* from Costa Rica were reported to germinate to lower percentages (13-28%) (Salazar, 2000) and to have lower MC (26%) (González, 1991) than those in my study, which germinated to 44%, and had a higher MC of 50%. My results for *Virola surinamensis* (MC=38.8%, Ger=48%) differ from those reported by Cunha et al (1995) for seeds of this species from Brasil (MC=26.5%, Ger=29%). Garwood (1983) reported yet higher germination (20-100%) for the same species from Barro Colorado Island, Panama. Despite differences in germination percentages, times for germination reported for seeds of *D. arboreus* and *V. surinamensis* support classifying them as having morphological (MD) and not morphophysiological dormancy (MPD). *Vochysia ferruginea* germinated to 35 % in my study, while germination reported by Gonzalez (1991), Rodriguez et al. (1997), and Salazar (2000) for selected seeds of this species from Costa Rica ranged from 80-90%. However, both populations were nondormant.

Most information about *Colubrina glandulosa* is for variety *reitzii*, from South America, and it is reported to have dormant (Queiroz, 1982; Ramalho Carvalho, 1994) or nondormant (Lorenzi, 1992) seeds. My results with *C. glandulosa* var *glandulosa* indicate clearly that the seeds have physical dormancy (PY) (Fig. 18 and cumulative germination curve in Appendix).

Seeds of *Chrysophyllum cainito* from Costa Rica seems to be dormant (Salazar 2002), at least part of them, while my results with Panamanian seeds clearly show that they are nondormant. *Hyeronima alcheornoides* is a colonizer species reported to have nondormant seeds (Garwood, 1983; Gonzalez, 1992) or to have "stepped" germination (Flores 1993a). My experiments show clearly that the seeds are dormant (MLG=52 days). Frequently, populations of the same species with a wide geographic range show significant variability in seed viability and germination (Vázquez-Yañez and Orozco-Segovia, 1990).

Only two species, *Spondias mombin* and *S. raldkoferii,* had higher germination percentages and better synchrony after dry storage (see cumulative germination curves in Appendix), which is described as afterripenning, a progressive loss of dormancy as a function of temperature and time in dry environments (Fenner, 2000). This mechanism, perhaps best known in Gramineae, is considered to be an adaptation to survive seasonal drought. Both *Spondias* species shed their seeds in the late rainy season, and the requirement for a dry period might insure that they germinate in the next rainy season. The requirement for a dry period to overcome dormancy also is supported by the fact that fresh seeds in my study, maintained in wet conditions in trays, had a total germination as low as 9 and 5% after 234 and 261 days, respectively, indicating most seeds did not afterripen. Garwood (1986b) got higher germination percentages in seeds of *S. monbin* sown on the surface than I did in my experiments, where the large seeds of *Spondias* were buried to half their size. The seeds exposed on the surface in Garwood's study could have dried to some degree between watering times; thus, allowing the seeds to afterrripen.

Eighteen species with mean or median length of germination around 30 days represent a challenge to decide whether or not their seeds are dormant. Baskin and Baskin (1998) defined dormant vs. nondormant seeds based on the time needed to initiate germination. The rate of germination represented by mean germination time was considered a promising parameter to study germination in trees (Bonner, 1998). I used the median time of germination as the arbitrary line to define dormancy. It represents the time taken to germinate for half of the seeds that germinated and was selected based on the right skewnees that is characteristic of germination curves of most species. Nevertheless, the right tail of the germination curve could be an indication of dormancy in the remaining seeds in the lot, especially if germination percentage is low. Thus, to define dormancy in some of the species I considered complementary information, if it was available, such as responses to pretreatments, seed characteristics, or germination percentage after storage.

One group is represented by species common in the mature forest, with large seeds, high moisture content, and short longevity, that are not expected to be dormant. *Carapa guianensis* was reported to take 6 weeks to germinate (Record and Hess, 1986) and to have rapid germination ( 15-20 days) (McHargue and Hartshorn, 1983). In my results, based on the median (MLG=21 days), seeds of this species were considered to be non-dormant.

However, the mean length of germination (Mean LG) was 33 days, and they continued germinating for159 days after they had been sown (see cumulative germination curve in Appendix). Thus, at least some of the seeds in the lot were dormant. *Dipteryx olei*fera seeds from Costa Rica are described as nondormant (Flores, 1992), while my seeds from Panama had a MLG of 38 days, longer than the mean (Mean LG=33 days). *Prioria copaifera* is described as nondormant by Janzen (1983) and as dormant by Garwood (1983). My results agree with those of Garwood. Sork (1985) described the special situation of the big seeded colonizer *Gustavia superba,* which has no preference for gaps to germinate and was dormant in the different gap situations where it was tested. My MLG of 31 days might be an underestimate, since counting was suspended once I began removing the germinated seeds, due to sprouting of small pieces of the cotyledons that remained in the trays. This cotyledonary reprouting was described by Dalling and Aizprúa (1997). I suggest that *C. guianensis, D. oleifera*, and *P. copaifera* to some extent have mechanical restriction to radicle emergence due to the woody testa or endocarp, which, following Baskin and Baskin (2004), could be classified as physiologically dormant (PD). These species and *G. superba* are dispersed in the rainy season, and their dormant period is not long enough to delay germination until the next rainy season. The ecological meaning of dormancy in these species is not clear. Large seeds are not dispersed very far, and thus rapid germination of all seeds would produce a bank of seedlings easily to locate by predators. The option of delaying radicle emergence might allow some seeds to delay germination until a more suitable time to establish and/or escape predation as seedlings.

A second group with special considerations is represented by *Apeiba tibourbou* and *Luehea speciosa*. Both species had MLG<30 days. They belong to the same family (Tiliaceae) and to genera known to have physical dormancy, and germination of both species is increased by scarification. Acuña and Garwood (1987) reported that scarification with hot water or with sulfuric acid increased germination significantly in seeds of *A. tibourbou*, and Salamao (2002) reported a significant effect of pretreatment with liquid nitrogen. Salamao considers *A. tiborbou* to have a variable number of "hard" (water impermeable?) seeds in the sample. In my experiments, treatment with hot water had no effect on germination, but germination in control seeds was prolonged until day 80, with 47% total germination. Similarly, germination of control seeds of *L. speciosa* was prolonged to day 94, with only

22% total germination. Germination of seeds of *L. speciosa* stored for 4 months increased significantly after treatment with hot water. I suggest that only a portion of the seeds of both species have physical dormancy at maturity, and this portion might increase with dry environmental conditions at time of dispersal. A critical moisture level at which the seed coat becomes water-impermeable during seed maturation is discussed for seeds of different species by Baskin and Baskin (1998), and this may explain dormancy of stored seeds of *L. speciosa*. Dispersal time for *Apeiba tibourbou* is reported to begin with the dry season and to extend to the rainy season, perhaps making it possible for the species to produce seeds with different dormancy states during the fruiting season (maternal effects). Further comparison of these species with congeners whose seeds are well known to be physically dormant may result in an understanding of evolution of physical dormancy in Tiliaceae, as was done for Anacardiaceae (Baskin et al., 2000).

In my study, seeds of *Lacmellea panamensis* in my study, sown in February germinated to 75%. At least half of the seeds were nondormant (MLG=29), and they lost viability after 1-month of storage. In Garwood's study, seeds of *L. panamensis* were dormant both times she sowed them: March and April. Nevertheless, most of her seeds were collected from the ground, and additionally, they were allowed to dry for 2 days before sowing them. Since Garwood's germination percentages were lower than the ones in my study, it is possible that desiccation sensitivity caused loss of viability of seeds in her study.

Underdeveloped embryos of *Heisteria concinnea* (Olacaceae) (Fig.31) and of *Amaioua corymbosa* (Rubiaceae) (Fig.32) are described in this thesis for the first time. Both families have been reported to have this type of embryo, but not these genera (Agarwal, 1963; Robbrecht et al., 1991).

Discrepancies in results of germination tests for tree seeds are primarily due to the wide genetic variation present in seed lots that come from natural populations (Bonner, 1998). Time and method of collection, germination test procedures, and maternal effects also should be taken into consideration. Thus, germination rates reported in this thesis represent a baseline value for seeds collected in the PCW.

**Nursery management constraints**

In seasonal tropical regions, time for planting is restricted to the beginning of the rainy season, and commercial-tree nurseries that depend on market seeds work basically from the mid-dry season until the rainy season is established. For restoration projects, nurseries should emphasize seed-collection efforts during months when the higher number of species is in fruit in order to take advantage of field workers and time. Overall, for restoration projects that involve the use of large numbers of native species about which little is known, there will be a considerable increase in nursery costs and time required for nursery production in comparison to commercial-tree nurseries.

To improve nursery production, germination pretreatments should be determined for those species that germinate to low percentages and/or at low rates, facilitating use of space and scheduling of seedling production. This is especially true if the species has an optimal field performance and is also a promising timber or agroforestry species.

If no pretreatment is applied, and considering MLG, dormancy, and desiccation sensitivity of seeds, there will be an "overlap" of time for seed collection and seedling production during most parts of the year. At the end of the dry season and the beginning of the rainy season (February to April approximately), there will be a peak of all activities in the nursery: collecting seeds, sowing seeds, and transplanting seedlings to containers. From the mid rainy season to the beginning of the next rainy season, space in the nursery will be used for both seeds in their germination beds and seedling in their containers, waiting for the next planting season.

**Dormancy and seed characteristics**

Seed size has higher variability than other traits and variables calculated for the species studied. Leishman et al. (1995) suggested that seed size is more strongly associated with other plant attributes than with environmental conditions for seedling establishment, resulting in a wide range of seed mass.

Seed mass and moisture content are weakly correlated, and neither is correlated with any of the germination variables. The majority of seeds weigh between 0.01 to 1 g (Fig. 5), and seeds >0.1g tend to have higher moisture content than seeds <0.1 g (Fig.8). However, although the correlation is significant it does not have predictive value. Time to germination,

its variation, and coefficient of variation of germination percentages are positively correlated, and all of them are negatively correlated with total germination percentage (Table 5). Thus, the more dormant seeds are, the less synchronous is their germination, and they germinate to lower percentages with a high coefficient of variation.

Within classes of dormancy, seeds with physical dormancy are the most consistent group. They tend to be smaller, drier, and less variable for the various characteristics measured. Nondormant seeds and those in other classes of dormancy are more variable in size and moisture content, with physiological dormancy being the most variable (Fig 33, 34).

Although longevity data from my study do not allow establishment either of the actual longevity of the seeds in the seed bank or in usual storage conditions, for 37 species it represents the first approach to their potential storage behavior, and few of the 90 species have been tested for longevity in storage. Many species have been labeled as recalcitrant just because they lost viability quickly, but this loss may be related to other causes such as poor seed-handling practices (Bonner, 1996). This is especially true for common tropical trees from natural stands, whose low density makes collection slow. Further, specific studies following international desiccation protocols are needed to determine which of the species with short longevity in laboratory storage conditions in this study can be considered to be desiccation-sensitive, especially those for which the reports are new. Only three of the 35 short-lived species are reported to be desiccation tolerant, and 21 had no previous record. Thus, the longevity data in this thesis for these species can be considered as an indication of possible desiccation-sensitivity behavior in either the intermediate or recalcitrant category.

Desiccation sensitivity is more common in large, moist seeds of tropical rainforest trees than in trees in other biomes (Chin et al., 1989; Dickie and Pritchard, 2002). My data support the assumption for high moisture content of desiccation sensitive seeds, i.e. seeds with shorter longevity in storage tend to have higher moisture content (Fig. 11). The relationship with size is not as clear (Fig. 12). Desiccation sensitivity in seeds is also associated with nondormant seeds of rainforest tree species (Ng, 1978; Vázquez-Yañez and Orozco-Segovia, 1990) and is less frequent in dormant seeds. Tweddle et al. (2003b) describe the presence of desiccation sensitive seeds in 14% species with PD and 14% species with MPD, two of three species with MD, and only 1.4% with PY. In my results, seeds of all species with physical dormancy and the majority of those with non-dormancy are long lived (61.7%), whereas the

majority of seed with physiological (60%), morphophysiological (71.5%), and half of those with morphological (50%) dormancy are short or very short-lived (Fig. 38).

It has been stated that a majority of dominant trees of humid moist forest have nondormant seeds that germinate rapidly to produce a carpet of very slow growing seedlings (Msanga, 1998; Ng, 1978; Vázquez-Yañes et al., 2000). Nevertheless, there are some tropical recalcitrant species reported to have an underdeveloped embryo, such as *Minquartia guianesnsis* and *Virola kischnyi* (Flores, 1996), and thus morphological or morphophyiological dormancy. Seeds of *Carapa guianense* have been reported to germinate several month after dispersal (Flores, 1993b) and seeds of *Dipteryx panamensis* to be dormant in a reforestation project on abandoned farmland in Panama, showing dependence on shade for germination but growing better with higher light (Hooper et al., 2002). Two recalcitrant species of Lauraceae, *Beilschmiedia kweo* and *Ocotea usambarensis,* continued to germinate for 3 months and 7 weeks (Msanga, 1998), respectively, indicating that at least some seeds have physiological dormancy. There is no clear explanation for the presence of dormant embryos (if not underdeveloped) in at least a fraction of the population of seeds that are desiccation sensitive, which, in turn, implies a continuous metabolism. (Garwood and Lighton, 1990). Garwood (1983) suggests that there is no competitive advantage for selection of early emergence of shade tolerant species, and they germinate throughout the rainy season. Thus, no selective force appears to favor non-dormancy in shade tolerant species with desiccation sensitive seeds dispersed in the rainy season. Further, the association between desiccation sensitivity of large, moist seeds of shade tolerant species with dormancy might be favored by biotic evolutionary forces. These seeds would not dry in the shaded understory, while delay of germination would allow some seedlings to escape predation as part of the seedling bank.

The majority of large trees (63%) have nondormant seeds, and the majority of mid-size trees have dormant seeds (65%). My sample size for understory trees (6 species) may be not representative. This is also true for species with MD seeds, which are represented by only two species. More information is needed about embryos in tropical trees seeds. My sample size for species with PY is small, but the proportion of species with PY is similar to that in Baskin and Baskin (1998) for semievergreen forest trees (22%). Despite the small sample size for shrubs, the trend is for increase in PD as tree height decreases, and physical

dormancy is absent in the understory. In agreement with these results, Baskin and Baskin (1998) reported that PD is more common in shrubs than in trees in semievergreen forests and that PY is more important in trees than in shrubs.

There was no statistically significant difference in class of dormancy between colonizers (pioneers) and generalist (intermediate and shade tolerant) (Pearson Chi-Square $p > 0.05$) (Fig. 36). The small number of species with a confident classification as pioneers or non-pioneers (13 and 19, respectively) hinders interpretation, but Dalling et al. (1997) concluded that pioneers on Barro Colorado Island (Panama Canal Watershed) exhibit a variety of seed sizes, seed dormancy patterns, timing of reproduction, and seed dispersal agents. The pioneer/shade tolerant dichotomy (Whitmore, 1989) is best described as a continuum (Alvarez-Buylla and Martínez-Ramos, 1992). The majority of species native to the PCW fell in a narrow range of intermediate values for demographic variables (Condit et al., 1996b). These authors proposed that this larger intermediate (building phase) group of species might be an indication of the need to take into consideration distributional, physiological, morphological, phenological, and demographic information to classify species into functional types that represent a multidimensional axis. The adaptive role of the different classes of seed dormancy within them could vary with the different combinations of traits, and further studies are needed.

**Dormancy class and seasonality**

In this section of the discussion, I will focus on understanding the adaptive significance of a delay in germination and its relationship with the different kinds of dormancy sensu Baskin and Baskin (2004).The proportion of dormant species I found for trees from the whole PCW (48 % of 94 species) was slightly smaller than that found by Garwood (1983) for Barro Colorado Island (50% of 157 species) and that found in compilations of several reports on semievergreen forests: 54% of 209 species (Baskin and Baskin, 1998) and 52% of 515 trees (Baskin and Baskin, In press).

The proportion of the different classes of dormancy I found in the whole PCW (ND=52%, MD=2%, MPD=7%, PD=25%, and PY=14%) (Fig. 16) differs slightly from the proportions found by Baskin and Baskin (1998) (ND=46%, MD=1%, MPD=7%, PD=30%, PY=16%) for a sample of 209 species, or by Baskin and Baskin (In press) (ND=52%,

MD=2%, MPD=6%, PD=28%, and PY=12%) for a later compilation of 515 tree species. Since the distribution of length of dormancy is a continuum (Garwood 1983), and dormancy definitions actually highlight that it is not an all or nothing trait but a continuum (Baskin and Baskin, 2004), the proportion of dormant and nondormant seeds will vary depending on the arbitrary line drawn to define dormancy from non-dormancy. *Chrysophyllum cainito, Hyeronima alcheornoides, Carapa guianensis, Dipteryx oleifera,* and *Prioria copaifera* are examples of species whose seeds have been considered to be both dormant and nondormant in different studies with seeds from different provenances and tested in different conditions (see above). Moreover, the slight differences between my study and those by Baskin and Baskin seem to fall not only on the arbitrary limit between dormancy and non-dormancy but also into the specific need of information about the presence of underdeveloped embryos and impermeable seed coats.

Overall, large, moist, short-lived, dormant seeds are more frequent in the rainy season, especially in the late rainy season (Fig. 10, 11, 13), with significant differences only for moisture content and class of dormancy. A longer germination time in the late rainy season agrees with the delayed-rainy syndrome described by Garwood (1983). She considered dormancy to be the primary mechanism controlling time of germination of seeds dispersed in the rainy season, and physiological dormancy appears to be the dormancy class of the majority of dormant seeds dispersed in the late rainy season (42.4% of total species, 73.7% of dormant ones) (Fig. 39, 40, Table 9). Moreover, physiological dormancy represents only 13% of the species dispersed in the dry season and only 17% of those dispersed in the early rainy season.

During the dry season, 47% of the total species dispersed were dormant, being distributed about equally within PY (19%), MPD (16%), and PD (12%). Garwood (1983) considered germination time for species dispersed in the dry season to be controlled equally by seed dormancy and dispersal timing. Physical dormancy appears to be favored slightly during this season. The majority of species with physically dormant seeds are dispersed in the dry (46%) and early rainy (39%) seasons. Only two of the 13 species (15%) were dispersed in the late rainy season, and both of hem species have a long fruiting period that includes the dry season. *Pseudosamanea guachapele* begins fruiting in the late rainy season and continues to

do so throughout the dry season, and *Ormosia macrocalyx* begins to fruit at the end of the dry season and continues to do so throughout the rainy season.

The majority of the species dispersed during the early rainy season are nondormant (62%), and the dormancy classes represented are PY (17%), PD (17%), and MD (4%). Following Garwood's (1983) interpretation, in the early rainy season the main mechanism controlling germination time is dispersal timing. Seed dormancy also is present, and both PY and PD appear to be favored equally. Nevertheless, from dry to rainy situations PY appears to decrease and PD to increase. This pattern resembles the geographical pattern of distribution of these two dormancy classes, discussed below.

The overall proportion of MPD is similar to that found by Baskin and Baskin (1998). Seeds of the majority of species (57%) with MPD seeds are dispersed in the dry season, 29% in the late rainy season, and 14% in the early late rainy season. Morphologically dormant seeds represent a very small proportion of the total species, which is similar to what Baskin and Baskin (1998) reported. One of the two species with MD is dispersed in the early rainy season and one in the late rainy season.

Time of germination can be controlled not only by dormancy but also by time of dispersal. Dormancy is the main mechanism controlling germination in the late rainy season, where PD is more common than other dormancy classes, and the delay of germination is longer than in the dry and early rainy seasons. In the dry season, when both dispersal and dormancy appear to have the same relative importance in controlling germination time, the number of species with ND seeds almost equal that of species with dormant seeds, and PY appears to be slightly favored (40%) within dormancy classes. In the early dry season, dispersal timing is the main mechanism that controls germination, and ND seeds are favored. Garwood (1983) considered timing of dispersal and dormancy to be part of a drought-avoidance syndrome (Angevine and Chabot, 1979). Nevertheless, seed dormancy class might not be related to control of germination time. Seed germination does not need to occur at the optimal time for seedling establishment if selection on other stages of the life cycle, like pollination, seed development, and seed dispersal, is relatively more severe (Garwood, 1986a). Moreover, it was suggested that drought tolerance traits could be more common than suspected, as was reported for seedlings of *Licania platypus* on Barro Colorado Island (Tyree et al., 2002)

**Dormancy, seed longevity, and the precipitation gradient**

Overall, the results show an increase in the proportion of dormant species with a decrease in precipitation, which agrees with Baskin and Baskin (in press) (Fig. 39, Table 9). In the wettest region, 57% of the species are nondormant, and the proportion declines to 53% in the driest region. These numbers are intermediate to those given by Baskin and Baskin (in press) for rainforest and semievergreen forest (58, and 52%, respectively) and higher than those reported by the same authors in 1998 (46%) with a smaller sample size (209 species). The proportion of species with PD is fairly similar throughout much of the precipitation gradient (27%-29%), but it declines strongly in the driest region (21%). The proportion of species with MD is nearly constant and it is never important. The proportion of species with MPD increases with decrease in precipitation, from 6.3% to 9.4%, but the relationship is obscured by the high proportion in the wetter region, 2598-2835 mm of precipitation. PY is the only class of dormancy that shows a clear trend to increase with a decrease in precipitation, from 8 % in the wettest region to 15 % in the driest. These results suggest that the dry part of the moisture gradient is an environmental force that favors PY, as predicted by evolutionary models (Baskin et al., 2000; Van Staden et al., 1989). Nevertheless, it has been proposed that PY is an important adaptation of pioneers, whose seeds germinate in response to high-alterning temperatures as an environmental cue in gaps (Baskin et al., 2000; Vázquez-Yañez and Orozco-Segovia, 1990). The presence of pioneer species with physically dormant seeds would be favored in all forest environments, regardless of timing and amount of precipitation. Thus, further investigation towards classification of successional status of the species studied is needed.

Comparing proportions among species with dormant seeds (Fig. 41), PD and PY appear to follow patterns found by Baskin and Baskin (in press). PD shows an abrupt decline to the driest region, almost the same as in tropical deciduous forest (43%). Physical dormancy in the driest region is only half that found by these authors for tropical deciduous forest (32 vs. 56%). MPD and MD do not change across the gradient.

The driest side of the PCW receives only 300 mm less precipitation annually and its dry season is only one month shorter, than tropical deciduous forest described by Murphy and Lugo (1995). To obtain similar proportion of classes of dormancy to those compiled by

Baskin and Baskin (in press) for a deciduous forest, we should expect only PY to be favored as an adaptive strategy. These authors compiled information from tropical forests of different geographic regions of the world with different floristic compositions; thus, phylogenetic causes might influence the proportions observed. Further analysis in this direction would allow better comparison between my study and theirs.

In a comparison of three sites of the PCW that represent the wetter, medium, and driest portions of the range cover by inventory plots used in this study, the proportion of deciduous canopy is 14%, 28%, and 41%, respectively, but not all individuals of deciduous species are deciduous at the same time. Further, the peak fraction of deciduous individuals in the canopy is lower in the three sites (4.8%, 6.3%, and 24.3%, respectively) (Condit et al., 2000). Condit et al. (2000) highlighted the fact that only some individuals of the so-called deciduous species are deciduous, and that it was common for different individuals to be deciduous at different times and to different degrees. This variation might be typical of tropical trees in wet seasonal environments where soil water availability varies from year to year. Is dormancy also a trait that can vary with environmental conditions within the same tree species whose seeds are dormant?

The trend shown in Fig. 40 for longevity of seed matches theories about desiccation tolerance increasing as rainfall decreases (Tweddle et al., 2003b). The trend shown supports the assumption that longevity categories in this study are strong indicators of desiccation sensitivity.

Finally, I must consider that some of the gradient in dormancy in my sample might be caused by differences in forest ages, or some bias of the species in the sample to successional species, and not only to the environmental gradient. Inferring dormancy class from phenological, germination, or seed studies for more species, from Panama or other tropical forest would improve the sample size. Also, a more careful analysis including other variables such as demography, phenology, and moisture requirements of the species would allow me to examine the relationship between dormancy and other adaptive strategies.

# SUMMARY AND RECOMMENDATIONS

- This study presents information on the biology of seeds of 100 species native to the Panama Canal Watershed (PCW), 22 of them with no previous record in the literature.
- Variation in germination rates, median length of germination period (MLD), and the presence of short-lived seeds in a significant number of the species involved in any restoration project in the PCW will increase considerably both the nursery costs and time required for nursery production. In the seasonal tropical forest of the PCW, it is reasonable to expect approximately 50% of the species to be dormant. Thus, to improve nursery production pretreatments for successful germination should be determined for those species that germinate to low percentages and/or at low rates. This is especially true for species that have an optimal field performance.
- Seed collection should be carried on year round. There will be one peak of seedling production at the beginning of the rainy season and a special need for space to store seedlings of species with desiccation sensitive seeds during the late rainy and dry seasons.
- Seed mass and moisture content (MC) were weakly correlated, and neither was correlated to length of germination time or percentage of germination. Thus, they have no predictive value.
- Longevity of seeds stored at 20ºC in paper bags appears to be a good predictor of storage behavior (desiccation sensitivity). For 37 species, my studies represent the first approach to determining their potential storage behavior.
- Seed dormancy class (sensu Baskin and Baskin 2004) was determined for 94 species for the first time. Twenty-three (24.5%) of 94 species had physiological dormancy (PD), seven (7.4%) morphophysiological dormancy (MDP), two (2.1%) morphological dormancy, and 13 (13.8%) physical dormancy (PY). No seeds had combinational (PY+PD) dormancy.

  Proportions of the different classes of dormancy for the whole PCW differ only slightly from those found by Baskin and Baskin's (1998; In press) compilation of information from trees of semievergreen forests around the world.

- Seeds of at least 18 species represented a challenge with to regard their assignment to dormancy or nondormancy based on an arbitrary value of only one parameter. The proportion of dormant seeds and the degree of dormancy among seeds at maturity vary within the same species, probably due to maternal effects.
- The presence of afterripening in *Spondias monbin* and *S. raldkoferii* is reported for the first time. I suggest that it has an adaptive value for delaying germination until the next rainy season.
- The presence of underdeveloped embryos in *Heisteria concina* (Olacaceae) and *Amaioia corymbosa* (Rubiaceae) is reported for the first time.
- Within seed dormancy classes, physically dormant seeds tend to be small (i.e seed mass<0.1g), dry (MC< 16%), and long-lived (> 4 months). Non-dormant seeds and those in other classes of dormancy are more variable in size and MC, with physiological dormancy being the most variable.
- The proportion of species with physiological dormancy increases with a decrease in plant height from large trees to shrubs, and physical dormancy is absent in understory trees.
- There is no significant difference in proportion of dormancy classes between pioneers and non-pioneers.
- At least half of the species whose seeds have physiological, morphological, or morphophysiological dormancy appear to be desiccation sensitive, based on their longevity in laboratory storage conditions. These values are higher than expected by the paradigm that associates desiccation sensitivity with nondormancy of seeds of tree species of mature tropical rainforests.
- My results on seed germination at a regional scale agree with studies of Garwood (1983) at a community level in Barro Colorado Island in the PCW. Dormancy is the main mechanism that controls timing of germination of seeds dispersed in the late rainy season. Dormancy and dispersal time of nondormant seeds are of equal importance in controlling germination in the dry season, while dispersal time is the most important factor controlling germination in the early rainy season. Physiological dormancy is the most common class of dormancy for seeds dispersed in the late rainy season, and physical dormancy is the most important class in the dry season.

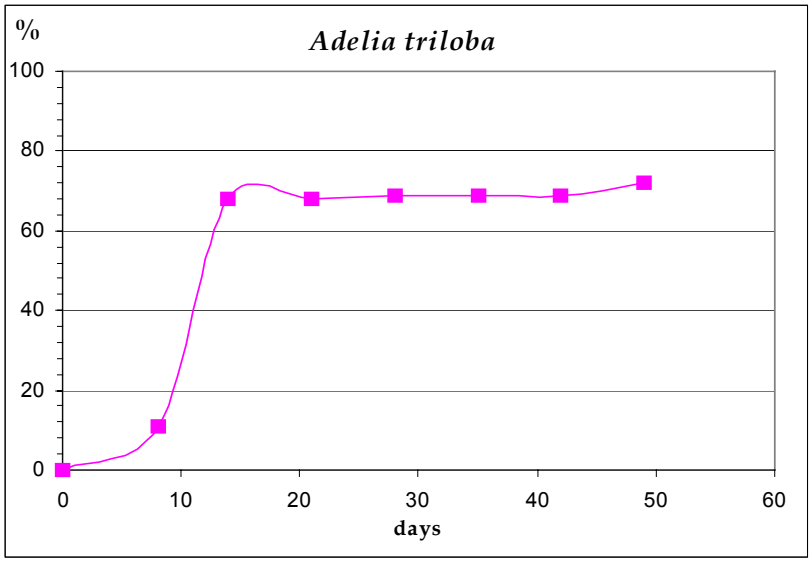
- Overall results indicate that the proportion of species with dormant seeds increase with decrease in precipitation, the proportion with physiologically dormant seeds decrease with decrease in precipitation, the proportion with physically dormant seeds increases with decrease in precipitation, the proportion with morphologically and morphophysiologically dormant seeds remains about the same, and the proportion with dormant seeds increases with a decrease in rainfall.
- The proportion of species with short and very short-lived seeds increases with an increase in precipitation, as expected, if these behaviors predict desiccation sensitivity of seeds.

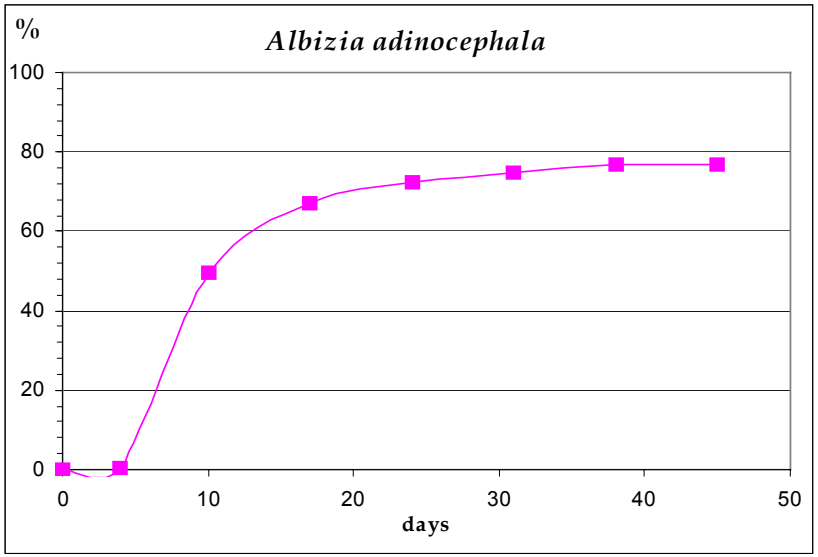
- Overall results indicate that the proportion of species with dormant seeds increase with decrease in precipitation, the proportion with physiologically dormant seeds decrease with decrease in precipitation, the proportion with physically dormant seeds increases with decrease in precipitation, the proportion with morphologically and morphophysiologically dormant seeds remains about the same, and the proportion with dormant seeds increases with a decrease in rainfall.
- The proportion of species with short and very short-lived seeds increases with an increase in precipitation, as expected, if these behaviors predict desiccation sensitivity of seeds.

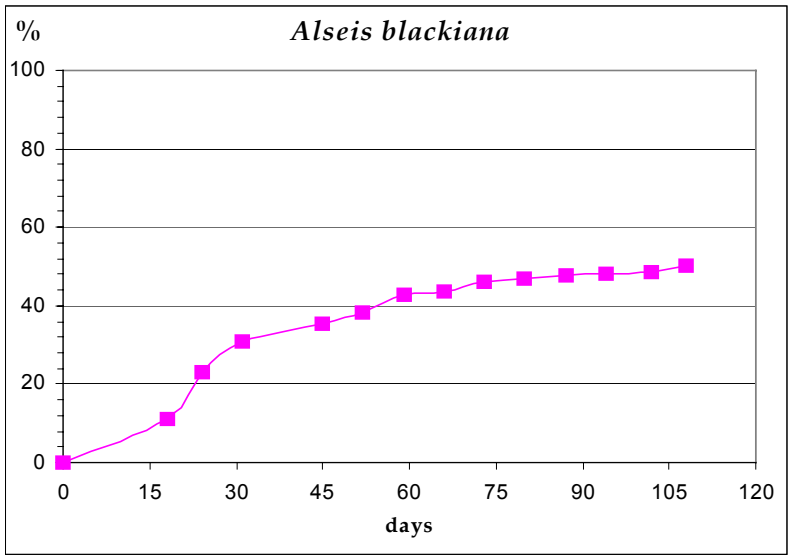
# APPENDIX

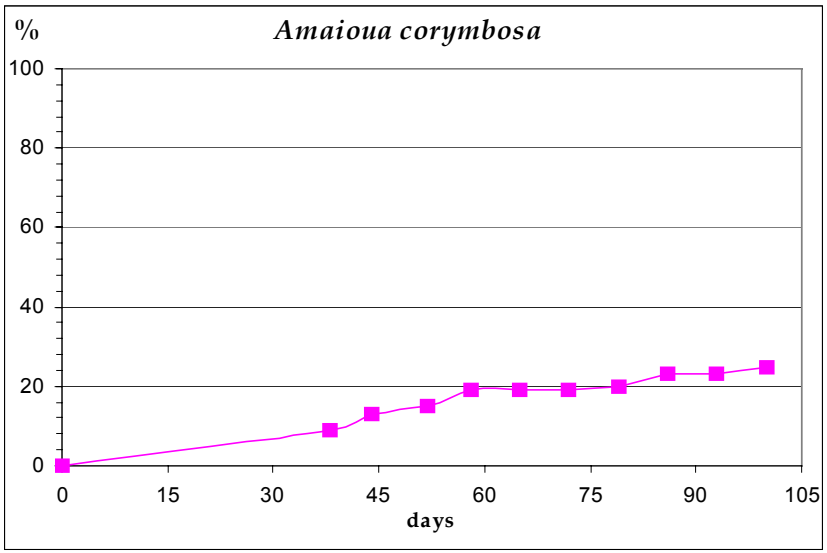
## CUMMULATIVE GERMINATION CURVES FOR 95 TREE SPECIES NATIVE TO THE PANAMA CANAL WATERSHED

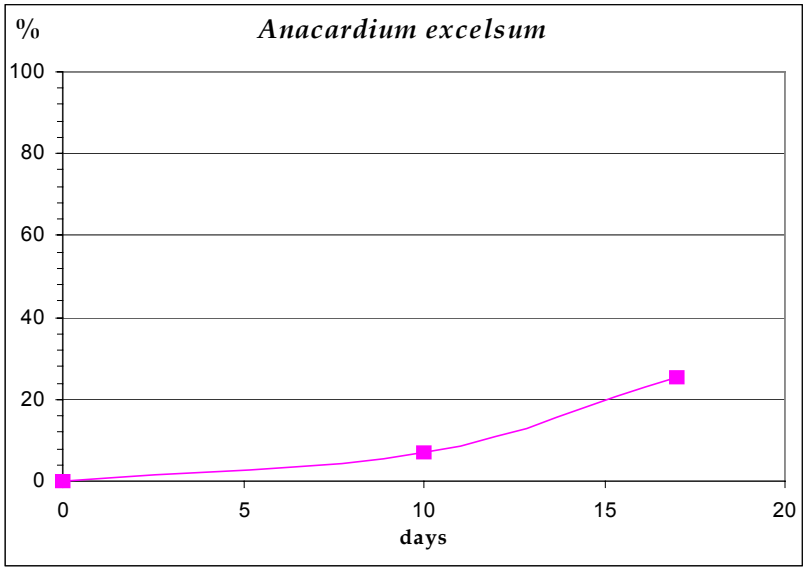
**(Alphabetically arranged by species)**

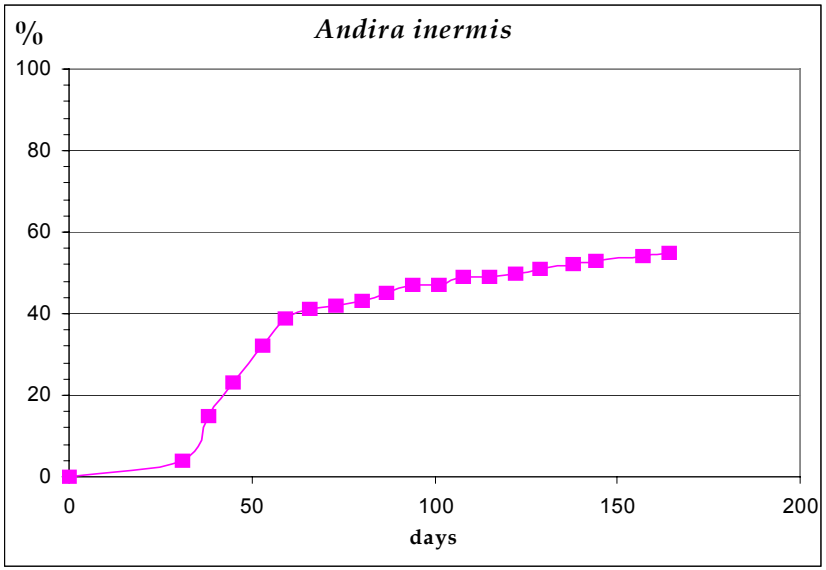

%
Adelia triloba
100
80
60
40
20
0
0
10
20
30
40
50
60
days

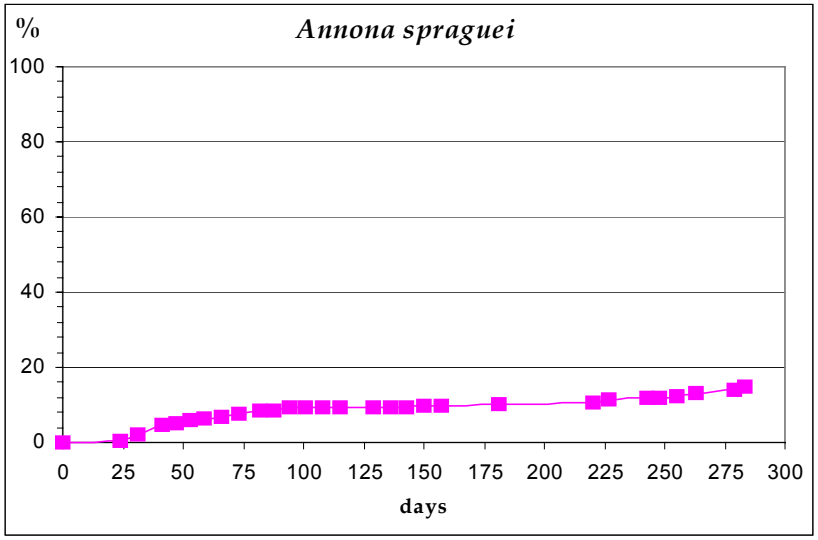

%
Albizia adinocephala
100
80
60
40
20
0
0
10
20
30
40
50
days

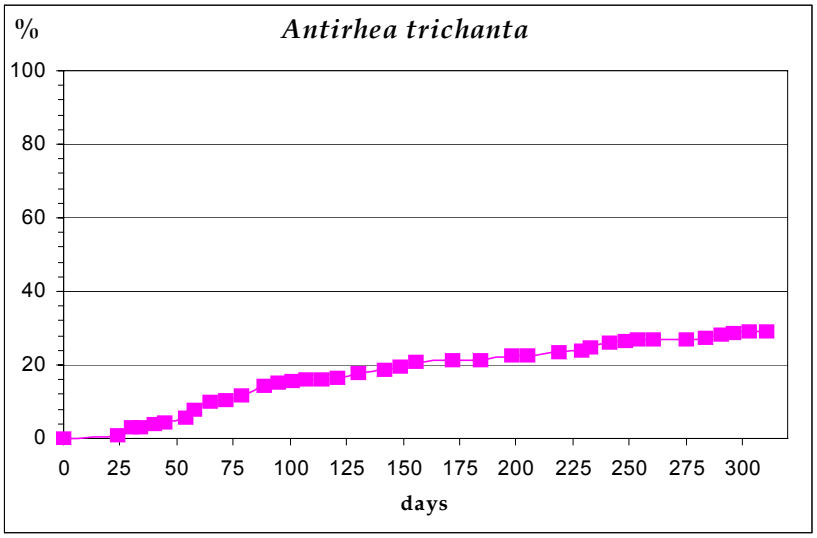

%
Alseis blackiana
100
80
60
40
20
0
0
15
30
45
60
75
90
105
120
days

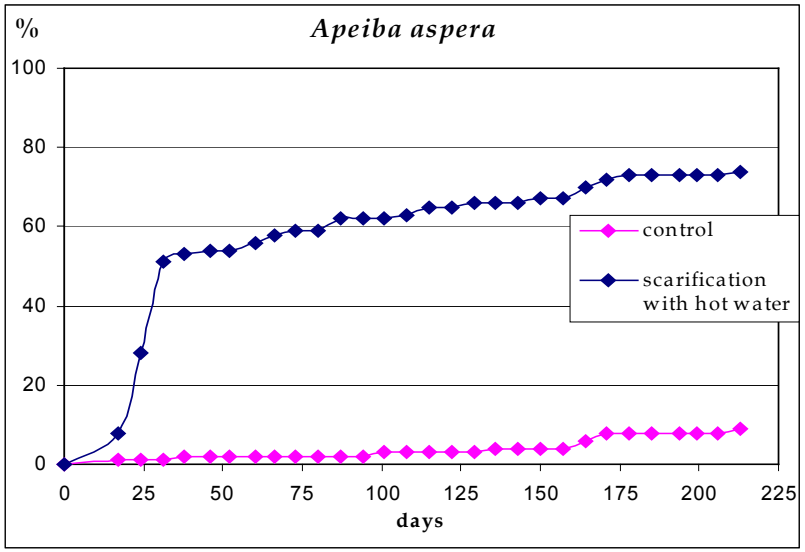

%
Amaioua corymbosa
100
80
60
40
20
0
0
15
30
45
60
75
90
105
days

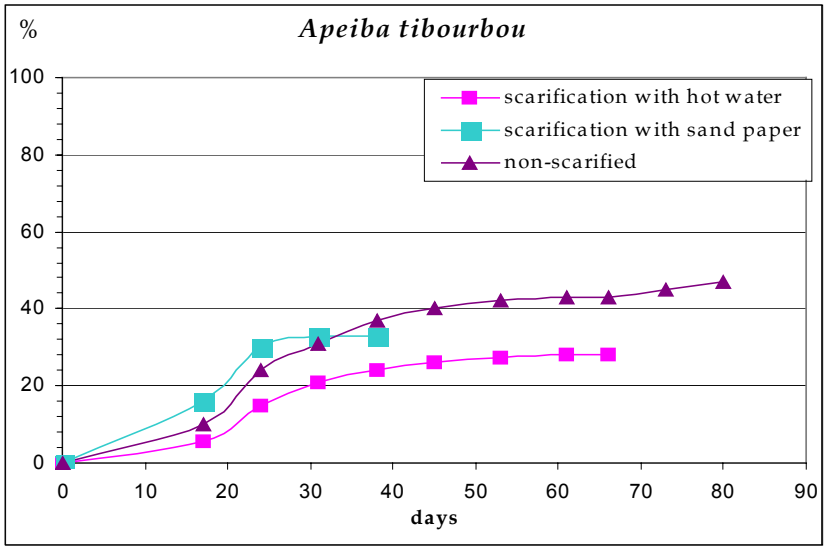

%
Anacardium excelsum
100
80
60
40
20
0
0
5
10
15
20
days

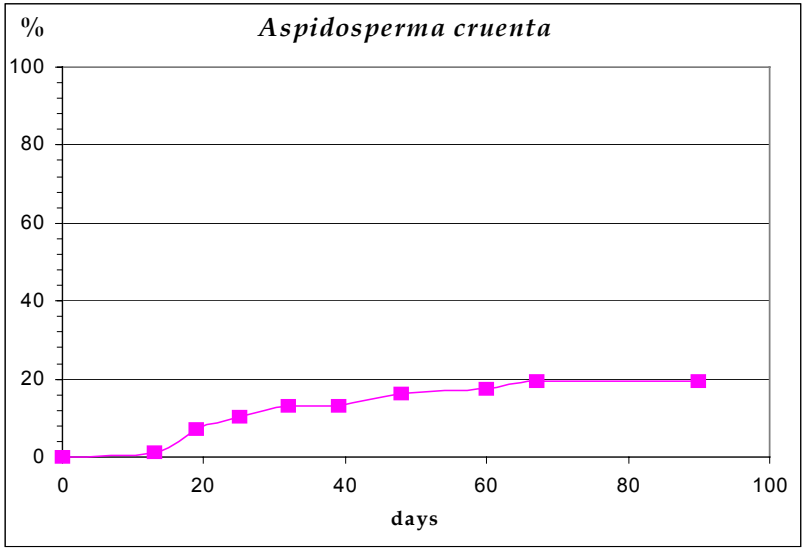

%
Andira inermis
100
80
60
40
20
0
0
50
100
150
200
days

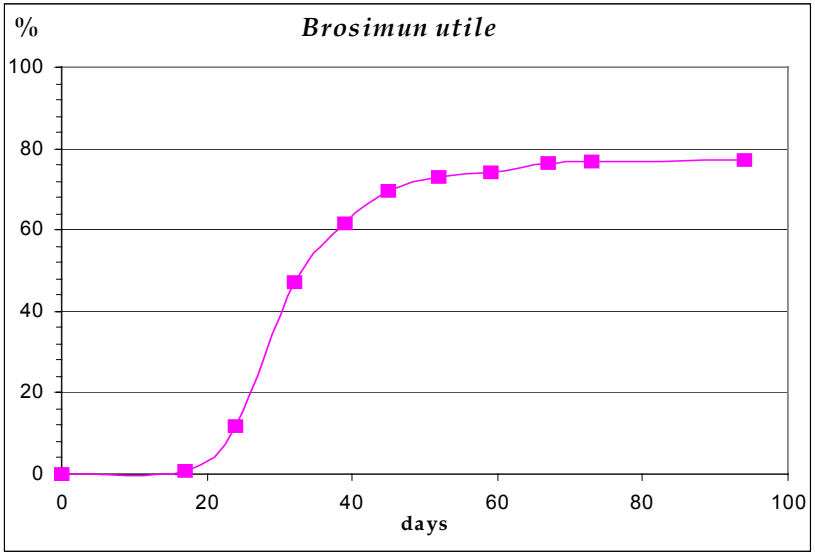

%
Annona spraguei
100
80
60
40
20
0
0
25
50
75
100
125
150
175
200
225
250
275
300
days

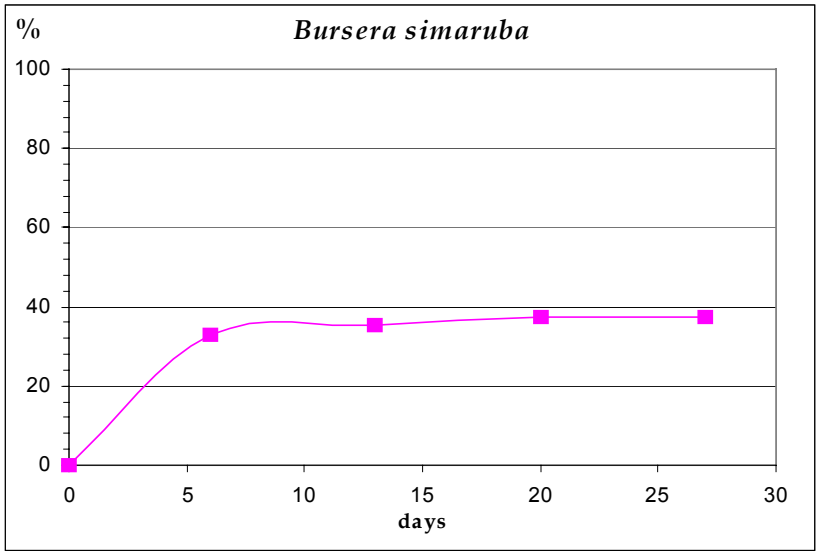

%
Antirhea trichanta
100
80
60
40
20
0
0
25
50
75
100
125
150
175
200
225
250
275
300
days

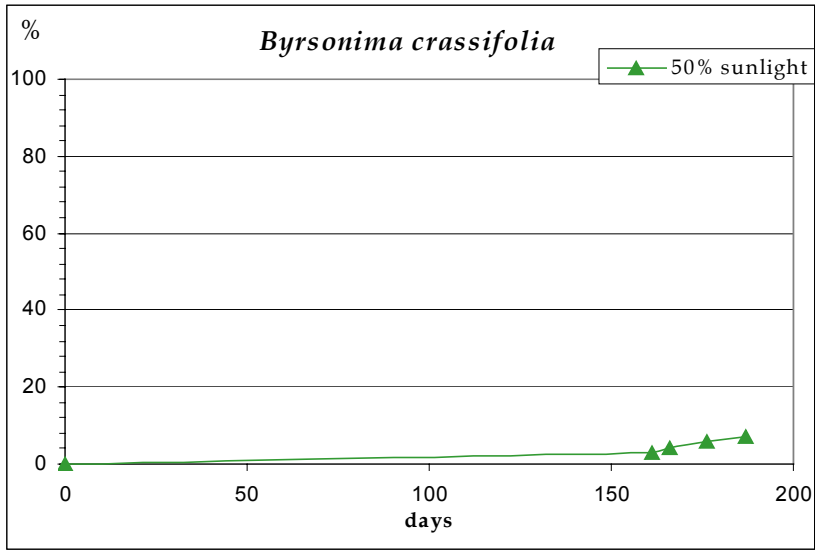

%
Apeiba aspera
100
80
60
40
20
0
0
25
50
75
100
125
150
175
200
225
days
control
scarification
with hot water

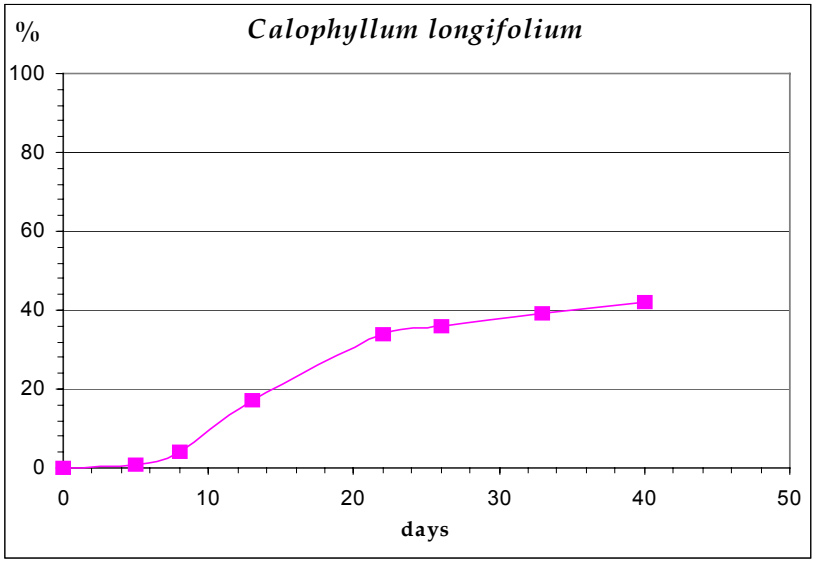

%
Apeiba tibourbou
100
80
60
40
20
0
0
10
20
30
40
50
60
70
80
90
days
scarification with hot water
scarification with sand paper
non-scarified

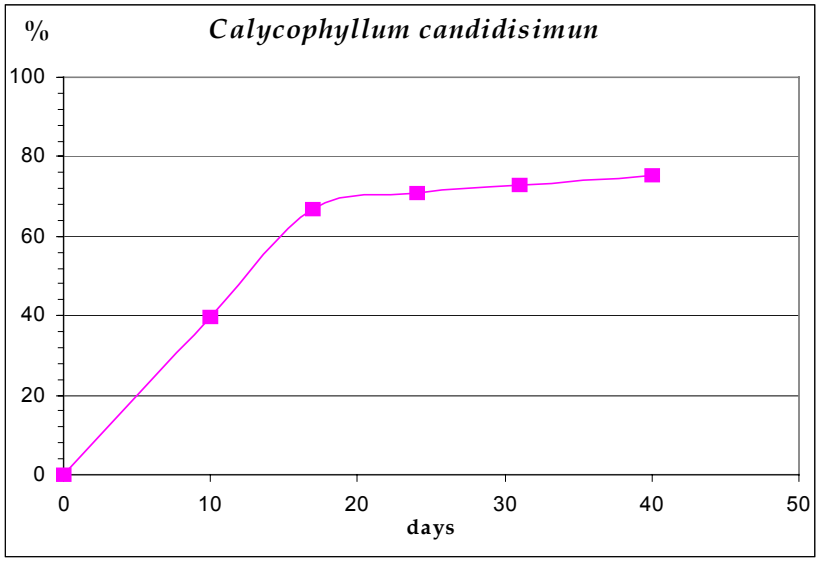

%
Aspidosperma cruenta
100
80
60
40
20
0
0
20
40
60
80
100
days

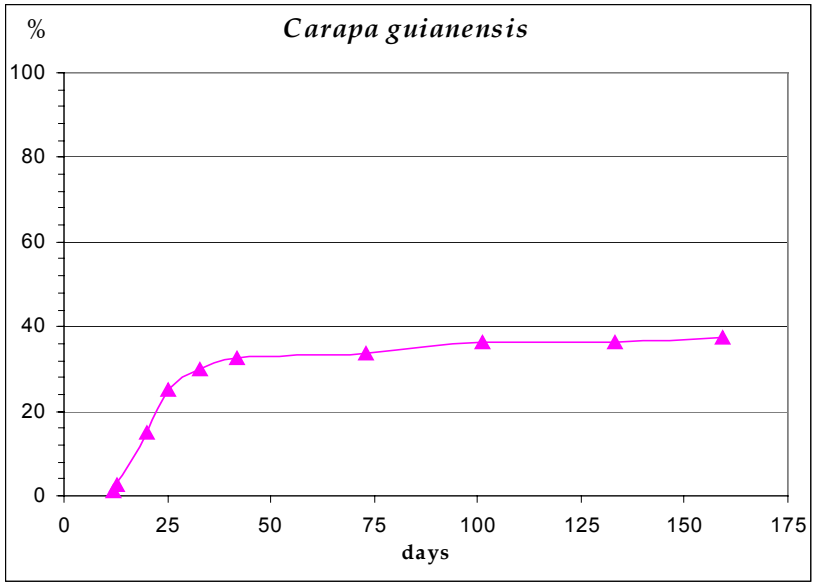

%
Brosimun utile
100
80
60
40
20
0
0
20
40
60
80
100
days

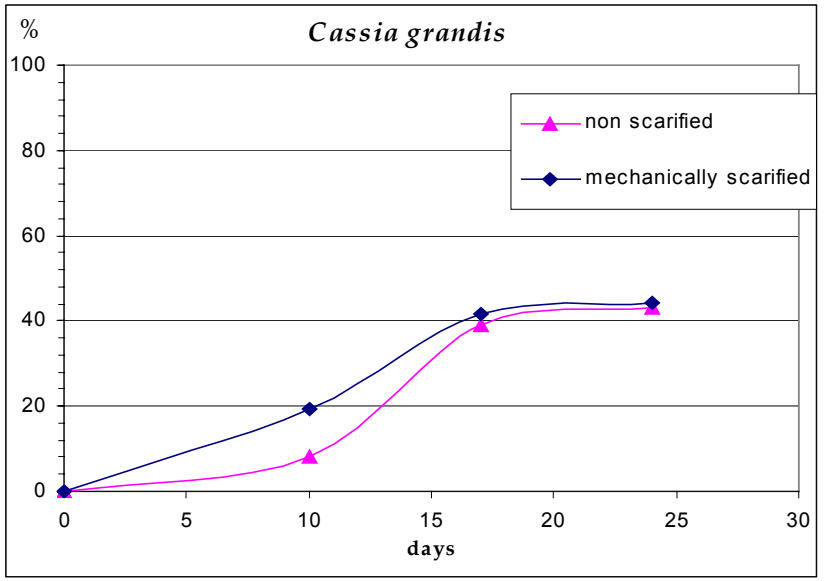

%
Bursera simaruba
100
80
60
40
20
0
0
5
10
15
20
25
30
days

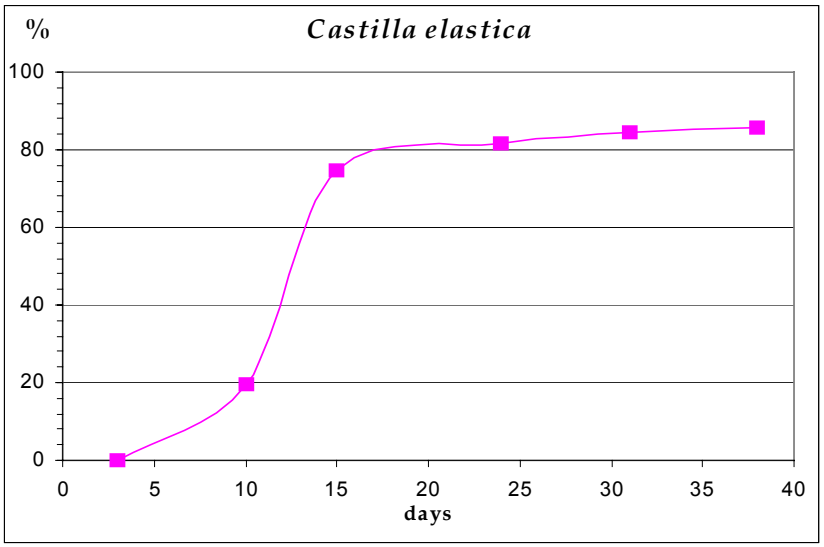

%
Byrsonima crassifolia
50% sunlight
100
80
60
40
20
0
0
50
100
150
200
days

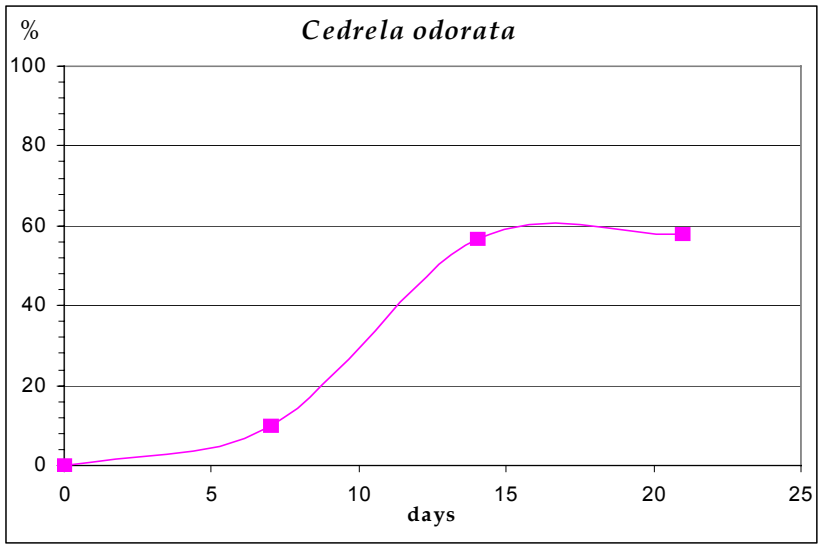

%
Calophyllum longifolium
100
80
60
40
20
0
0
10
20
30
40
50
days

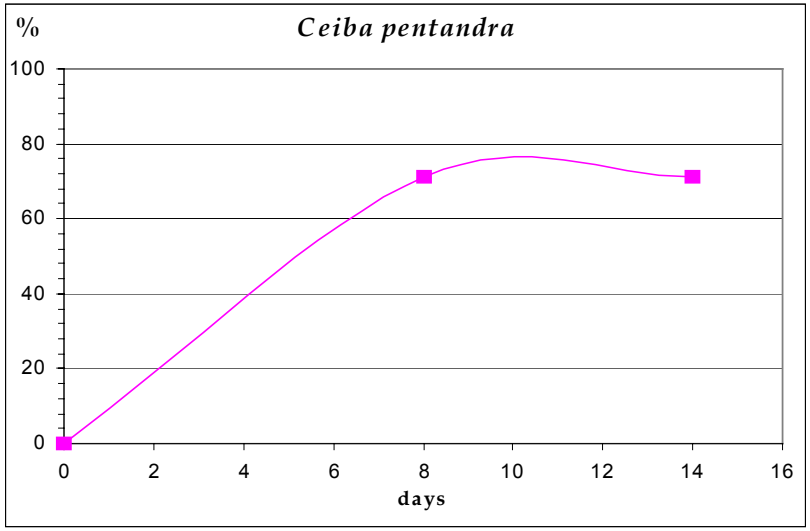

%
Calycophyllum candidisimun
100
80
60
40
20
0
0
10
20
30
40
50
days

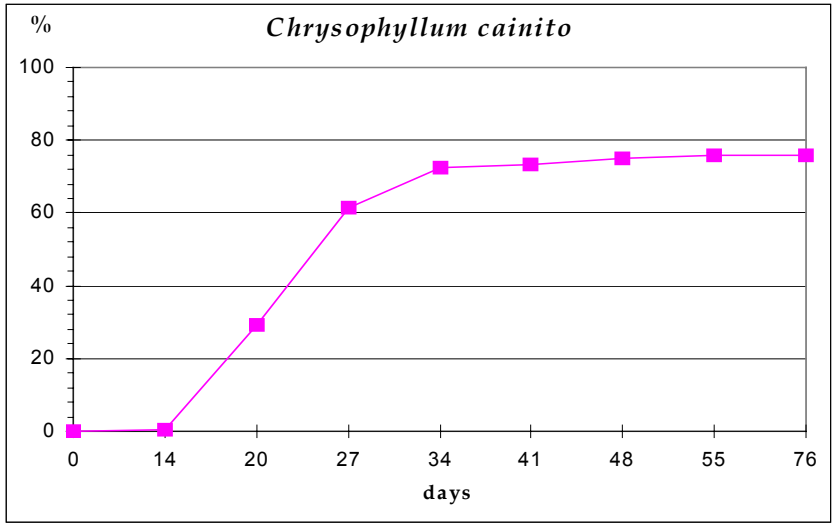

Carapa guianensis
%
100
80
60
40
20
0
0
25
50
75
100
125
150
175
days

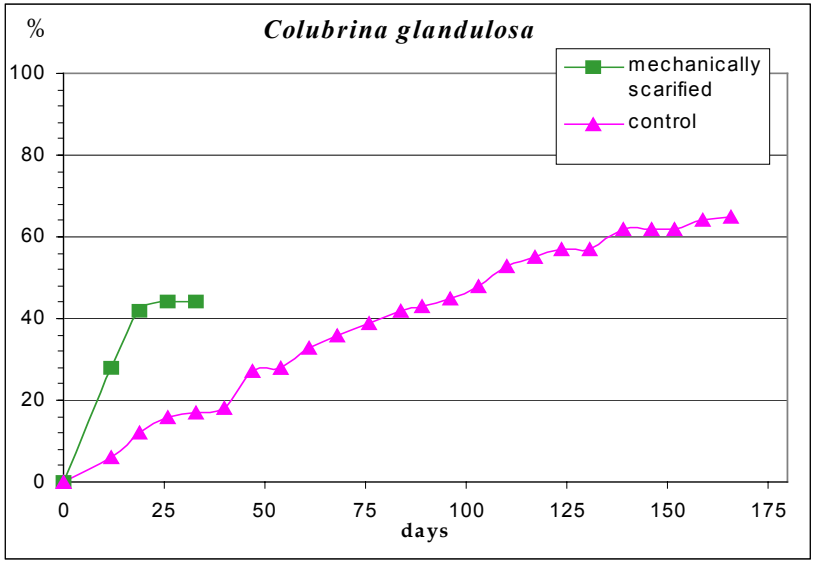

Cassia grandis
%
100
80
60
40
20
0
0
5
10
15
20
25
30
days
non scarified
mechanically scarified

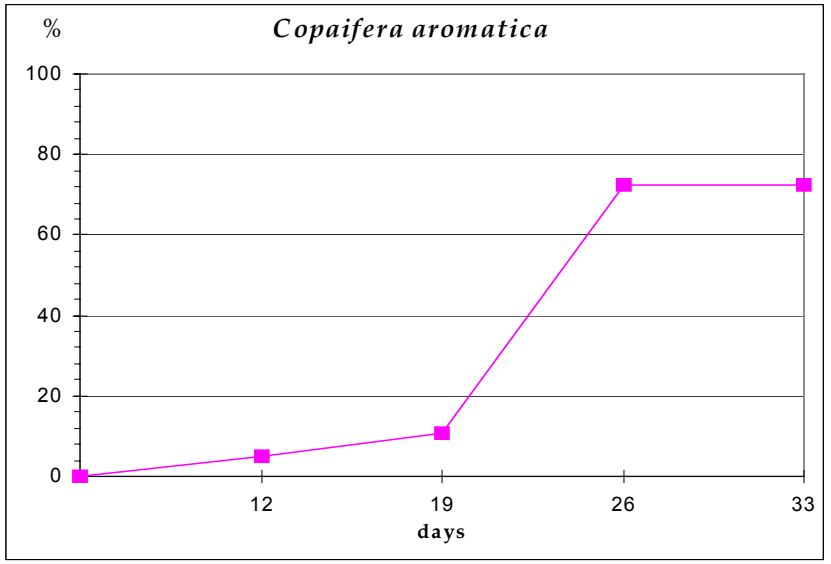

Castilla elastica
%
100
80
60
40
20
0
0
5
10
15
20
25
30
35
40
days

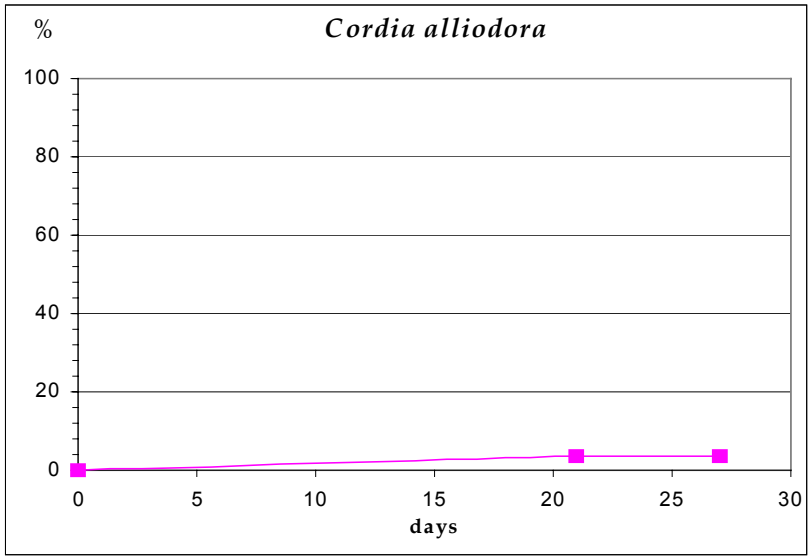

Cedrela odorata
%
100
80
60
40
20
0
0
5
10
15
20
25
days

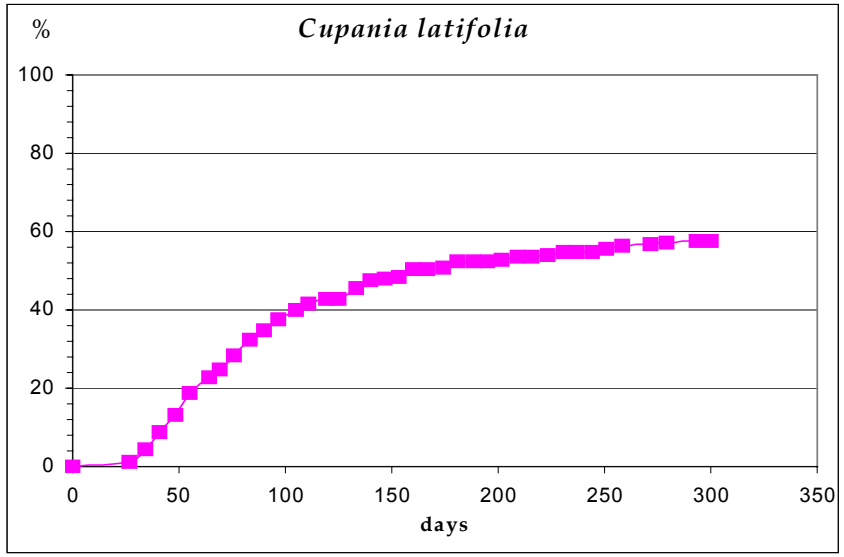

%
Ceiba pentandra
100
80
60
40
20
0
0
2
4
6
8
10
12
14
16
days

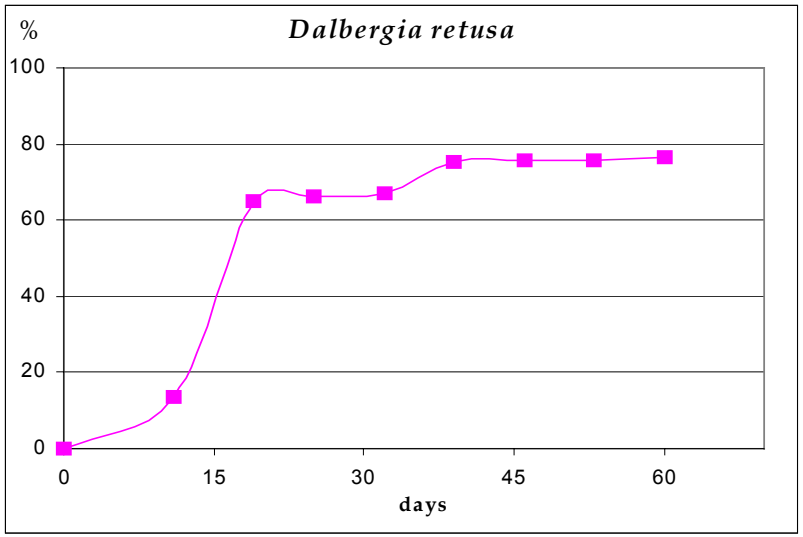

%
Chrysophyllum cainito
100
80
60
40
20
0
0
14
20
27
34
41
48
55
76
days

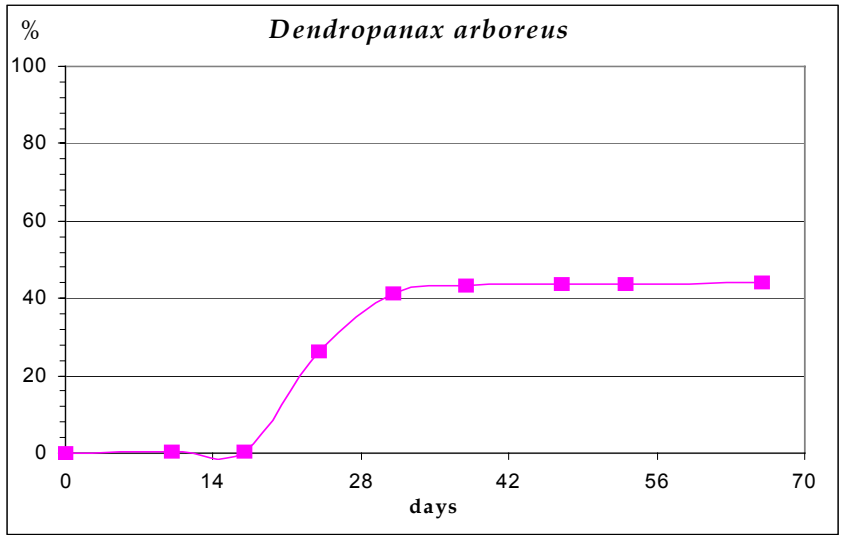

%
Colubrina glandulosa
mechanically scarified
control
100
80
60
40
20
0
0
25
50
75
100
125
150
175
days

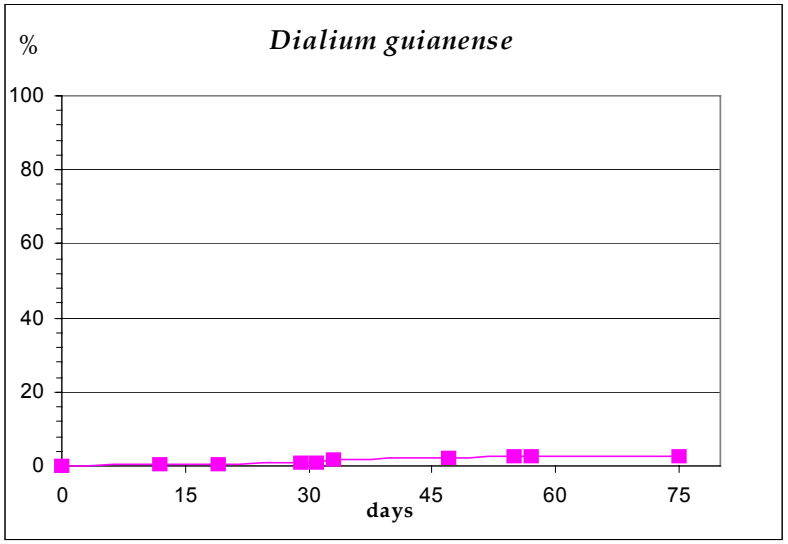

%
Copaifera aromatica
100
80
60
40
20
0
12
19
26
33
days

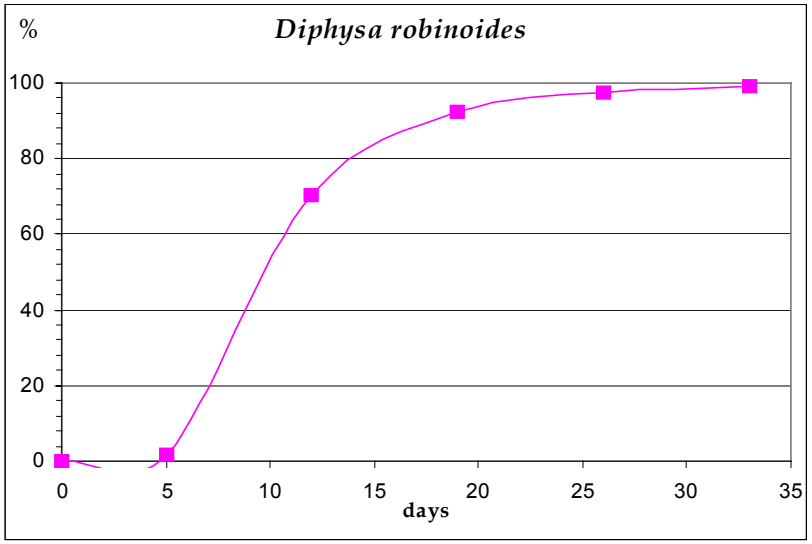

Cordia alliodora
%
100
80
60
40
20
0
0
5
10
15
20
25
30
days

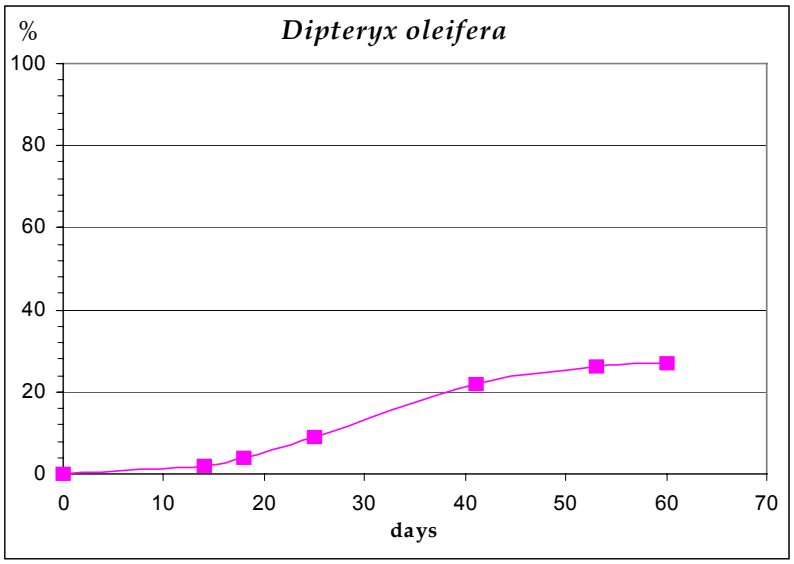

Cupania latifolia
%
100
80
60
40
20
0
0
50
100
150
200
250
300
350
days

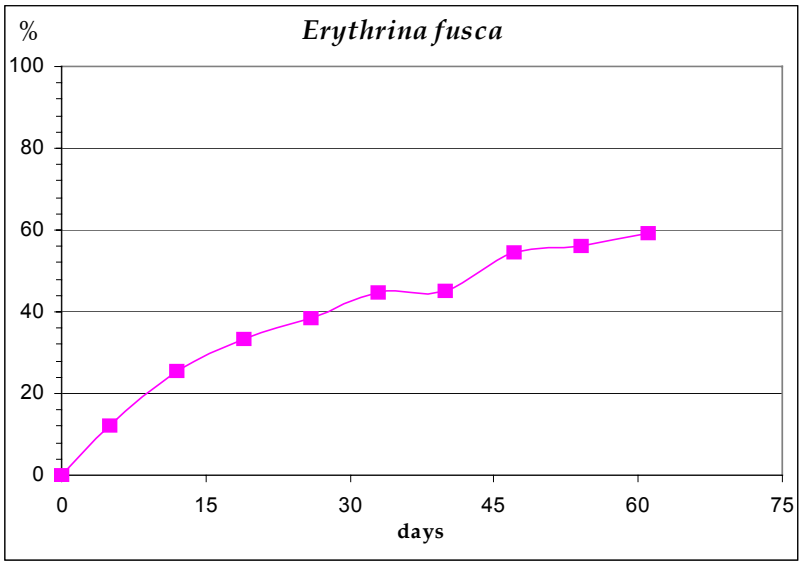

Dalbergia retusa
%
100
80
60
40
20
0
0
15
30
45
60
days

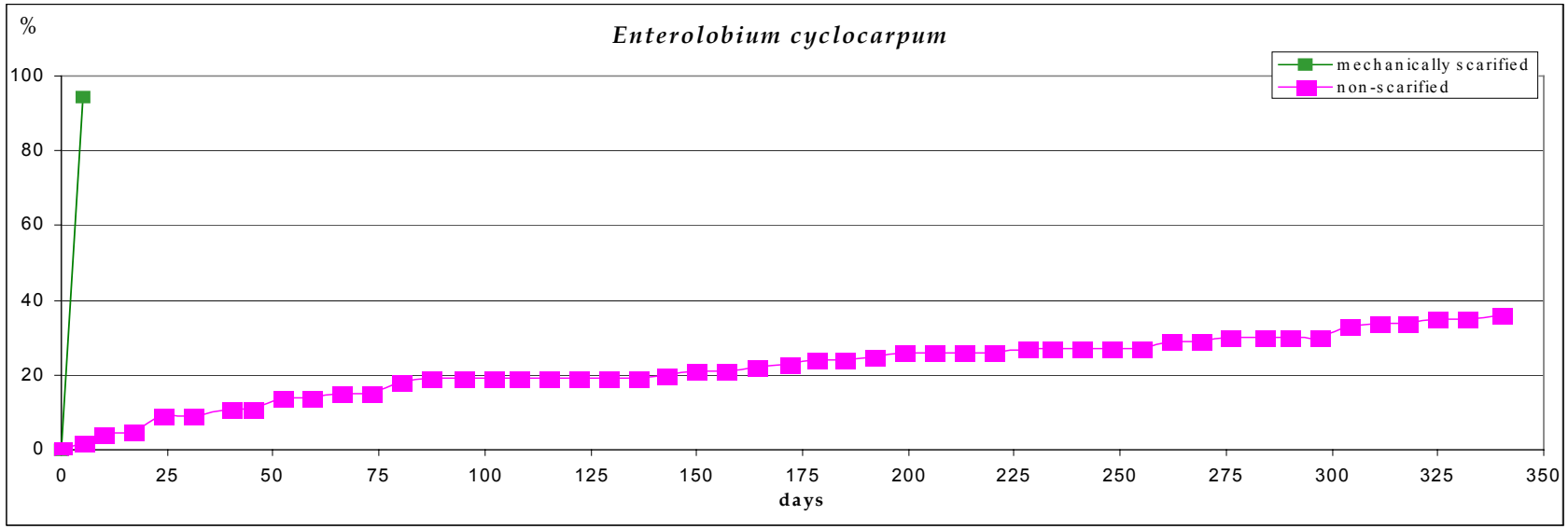

Dendropanax arboreus
%
100
80
60
40
20
0
0
14
28
42
56
70
days

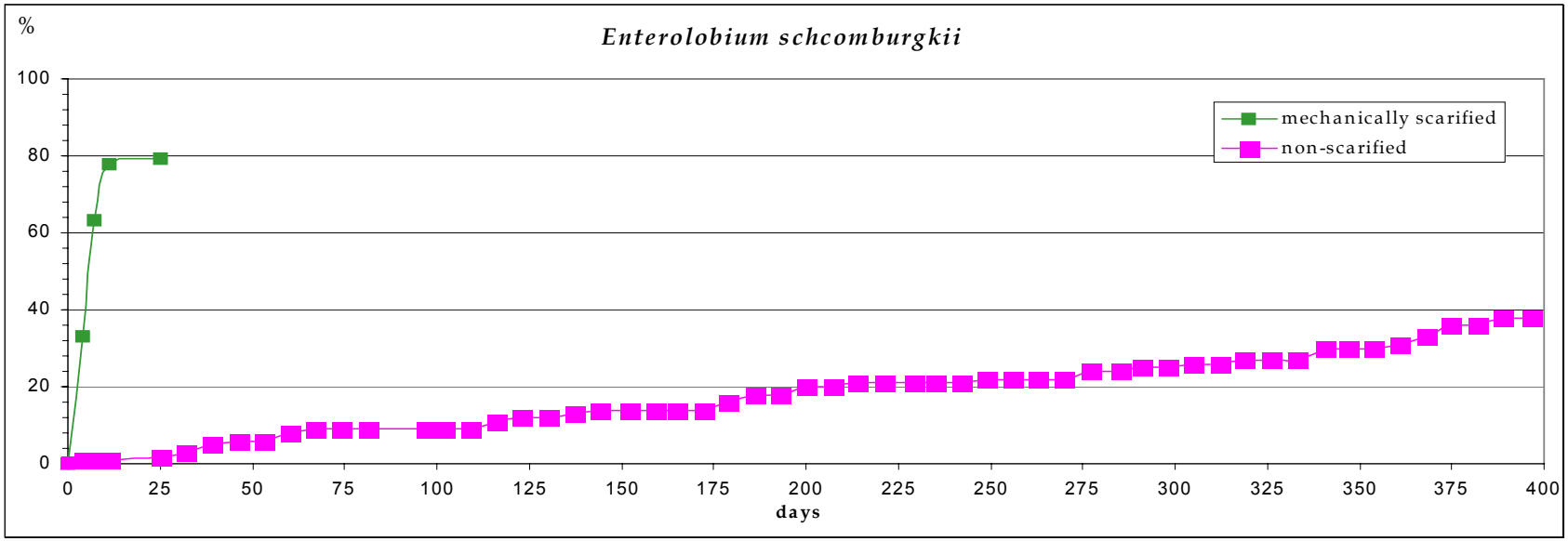

Dialium guianense
%
100
80
60
40
20
0
0
15
30
45
60
75
days

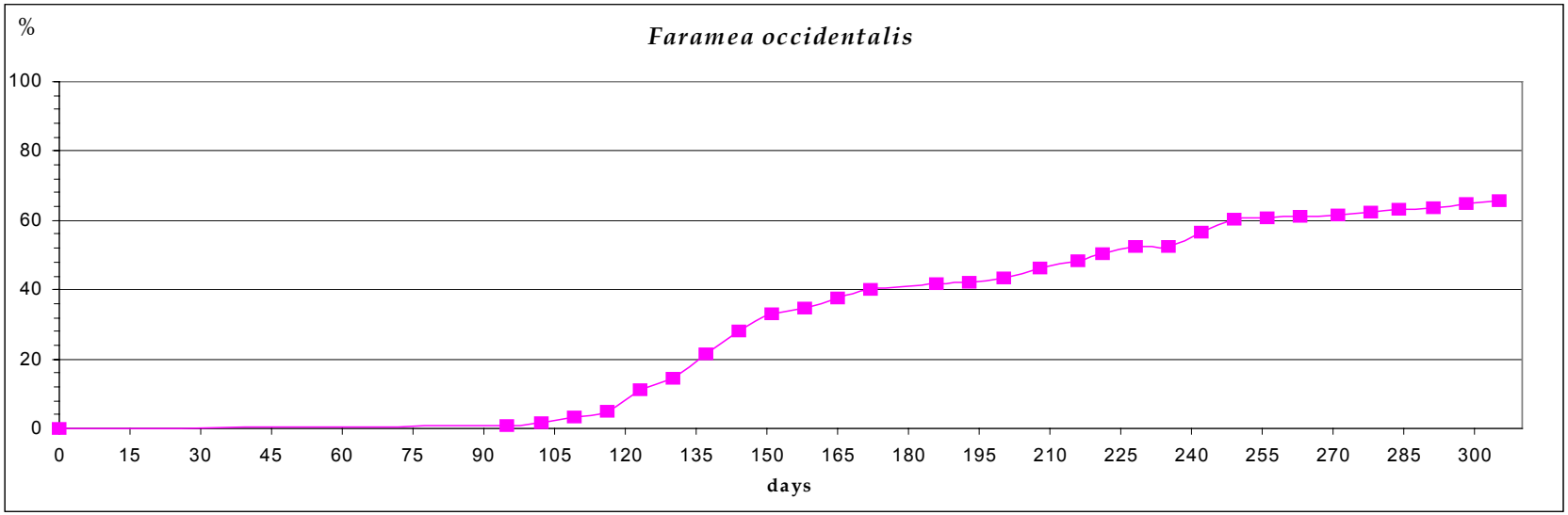

Diphysa robinoides
%
100
80
60
40
20
0
0
5
10
15
20
25
30
35
days

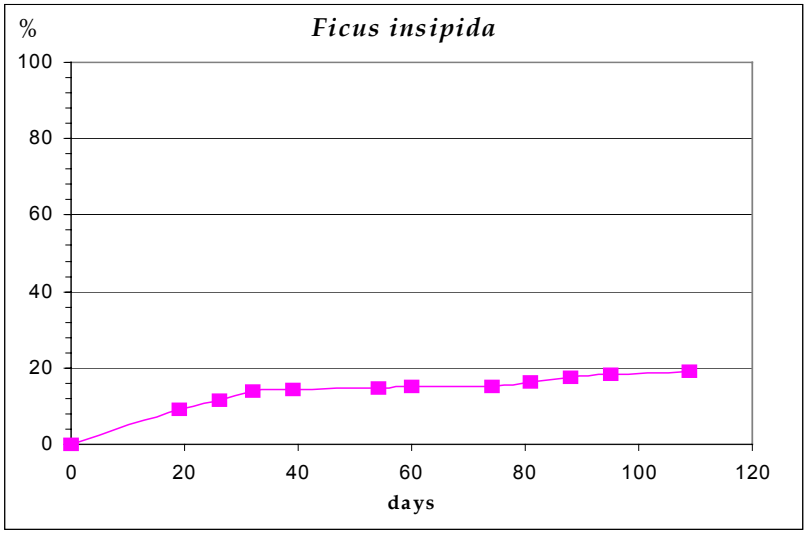

Dipteryx oleifera
%
100
80
60
40
20
0
0
10
20
30
40
50
60
70
days

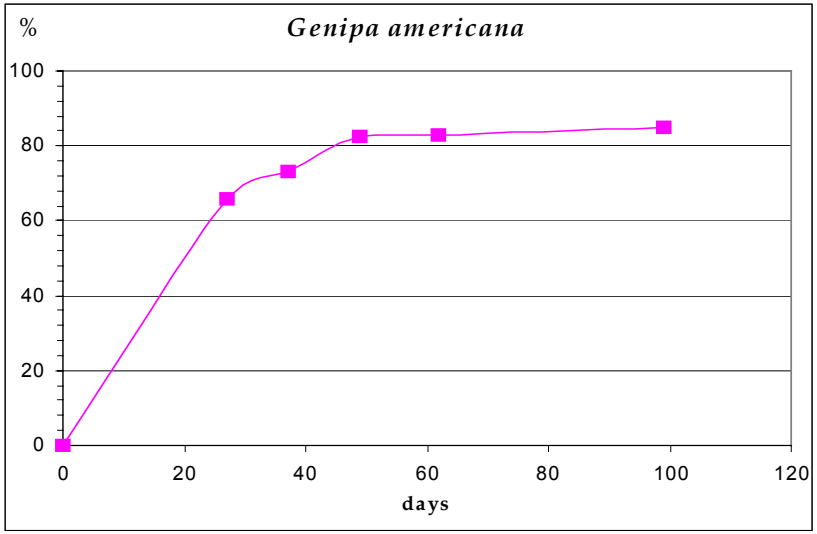

Erythrina fusca
%
100
80
60
40
20
0
0
15
30
45
60
75
days

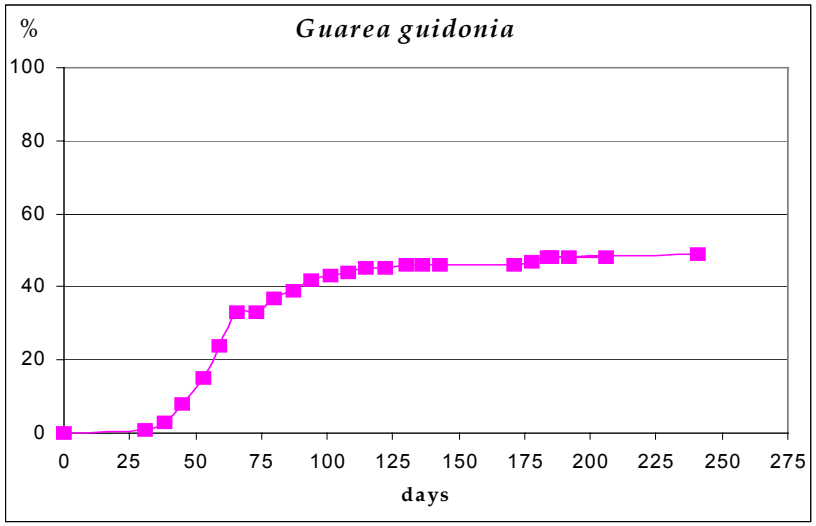

%
Enterolobium cyclocarpum
mechanically scarified
non-scarified
100
80
60
40
20
0
0
25
50
75
100
125
150
175
200
225
250
275
300
325
350
days

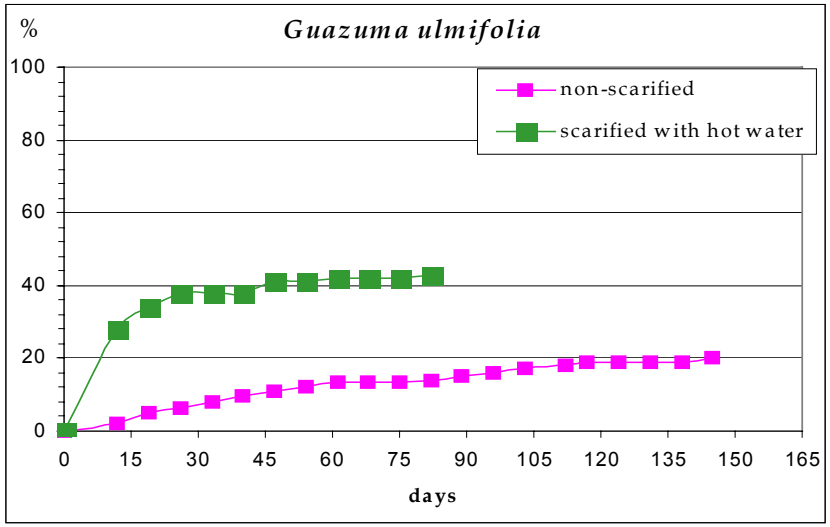

%
Enterolobium schcomburgkii
mechanically scarified
non-scarified
100
80
60
40
20
0
0
25
50
75
100
125
150
175
200
225
250
275
300
325
350
375
400
days

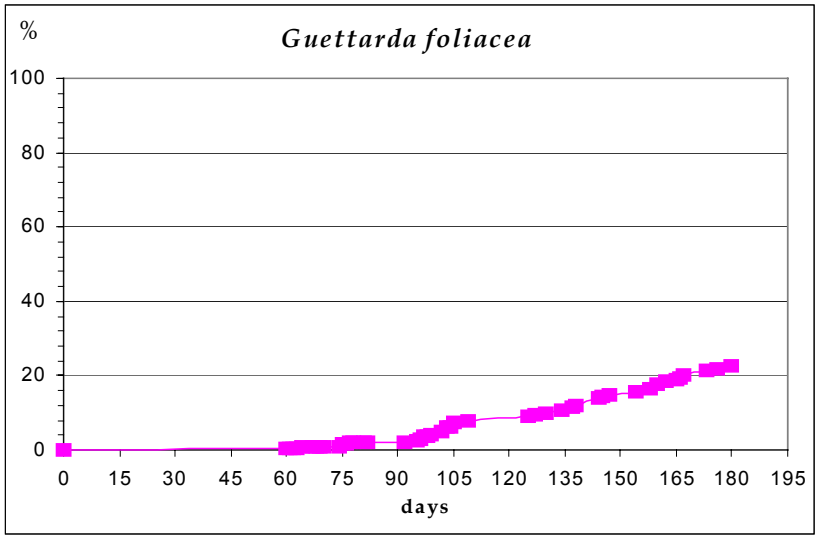

%
Faramea occidentalis
100
80
60
40
20
0
0 15 30 45 60 75 90 105 120 135 150 165 180 195 210 225 240 255 270 285 300
days

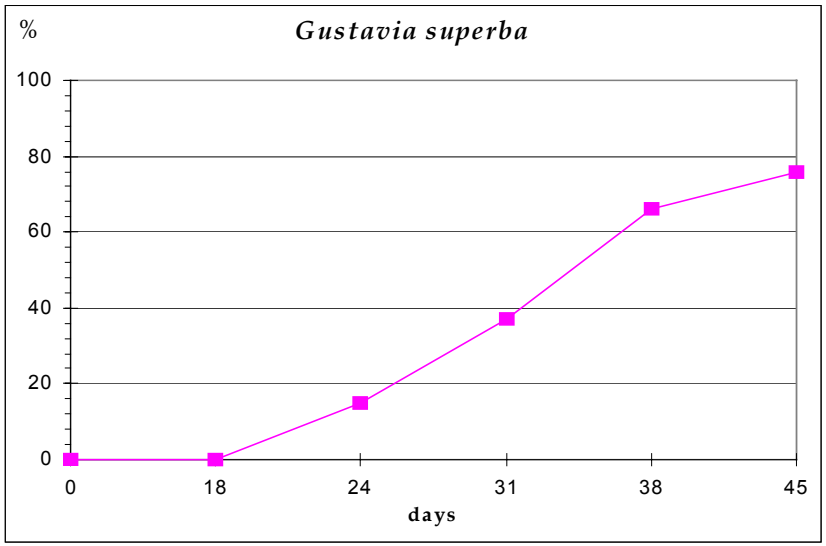

%
Ficus insipida
100
80
60
40
20
0
0 20 40 60 80 100 120
days

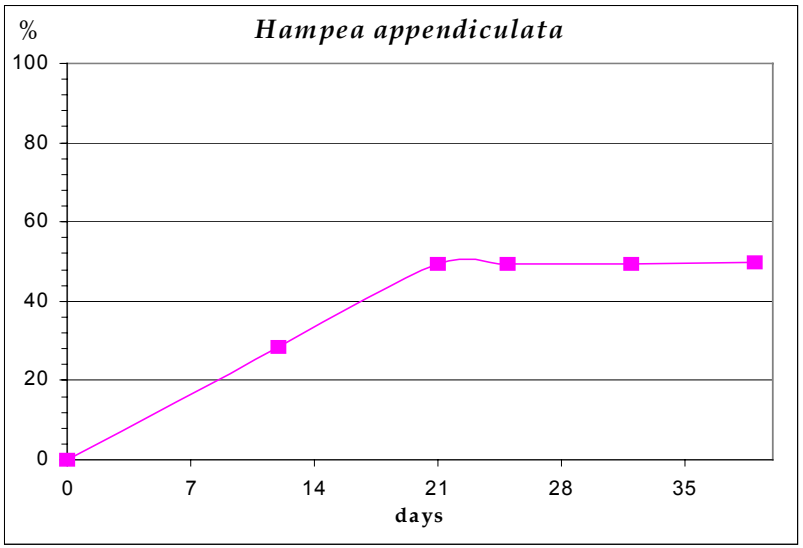

%
Genipa americana
100
80
60
40
20
0
0 20 40 60 80 100 120
days

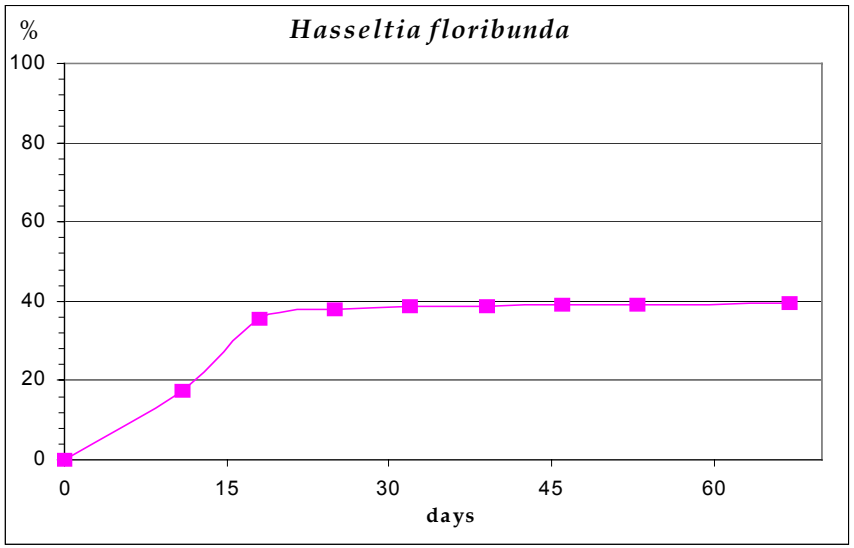

%
Guarea guidonia
100
80
60
40
20
0
0 25 50 75 100 125 150 175 200 225 250 275
days

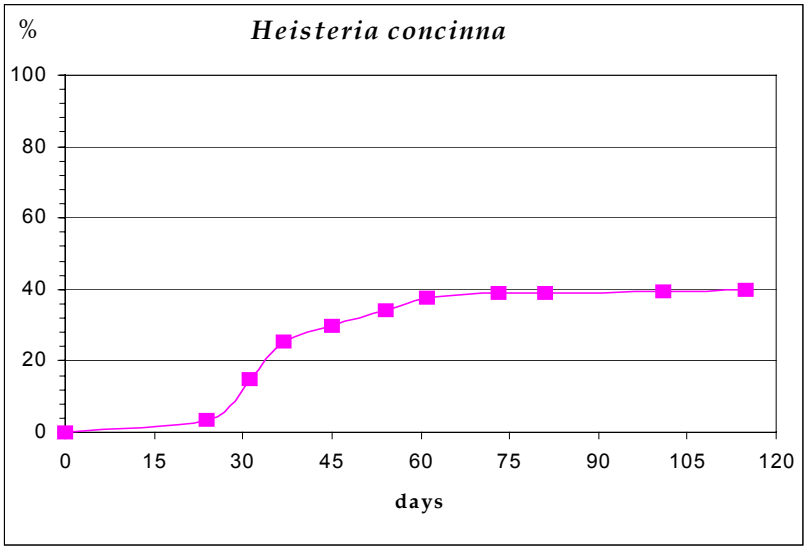

%
Guazuma ulmifolia
non-scarified
scarified with hot water
100
80
60
40
20
0
0 15 30 45 60 75 90 105 120 135 150 165
days

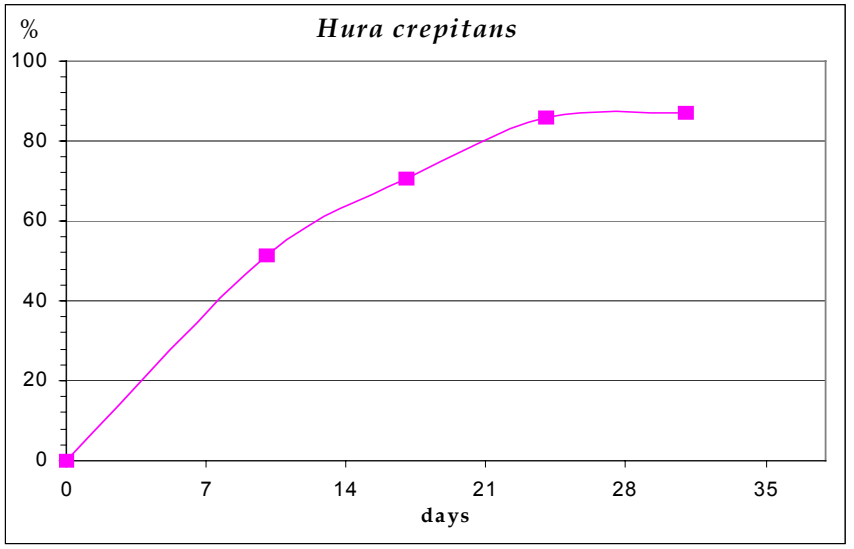

%
Guettarda foliacea
100
80
60
40
20
0
0 15 30 45 60 75 90 105 120 135 150 165 180 195
days

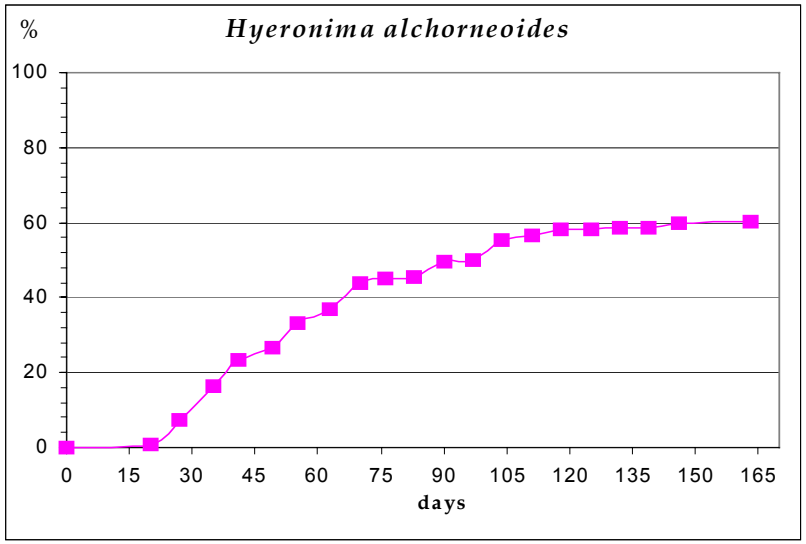

%
Gustavia superba
100
80
60
40
20
0
0 18 24 31 38 45
days

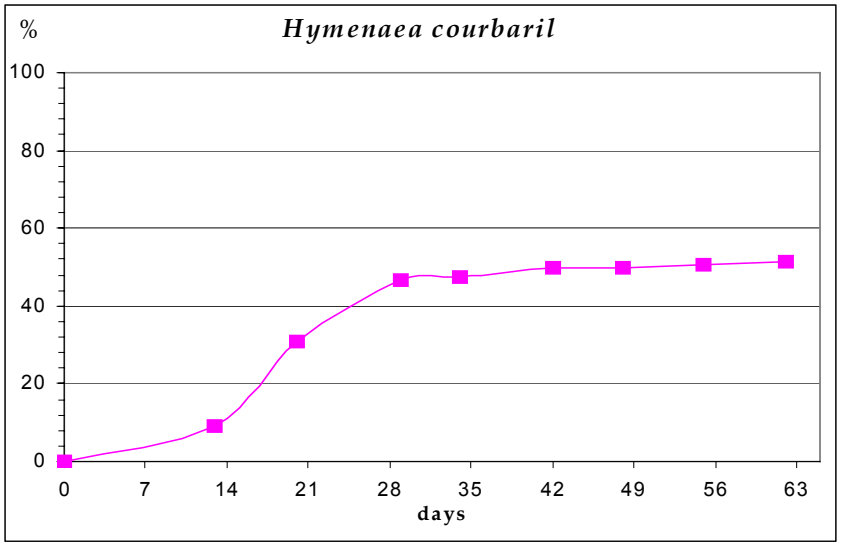

%
Hampea appendiculata
100
80
60
40
20
0
0
7
14
21
28
35
days

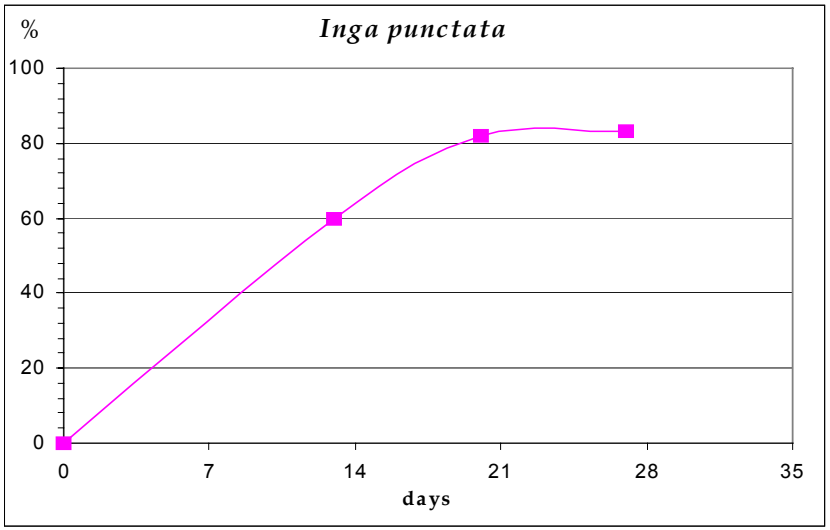

%
Hasseltia floribunda
100
80
60
40
20
0
0
15
30
45
60
days

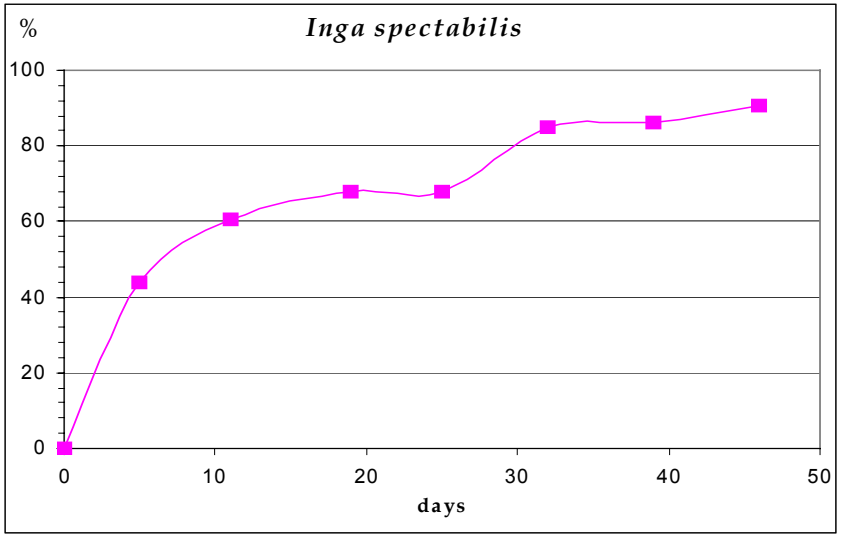

%
Heisteria concinna
100
80
60
40
20
0
0
15
30
45
60
75
90
105
120
days

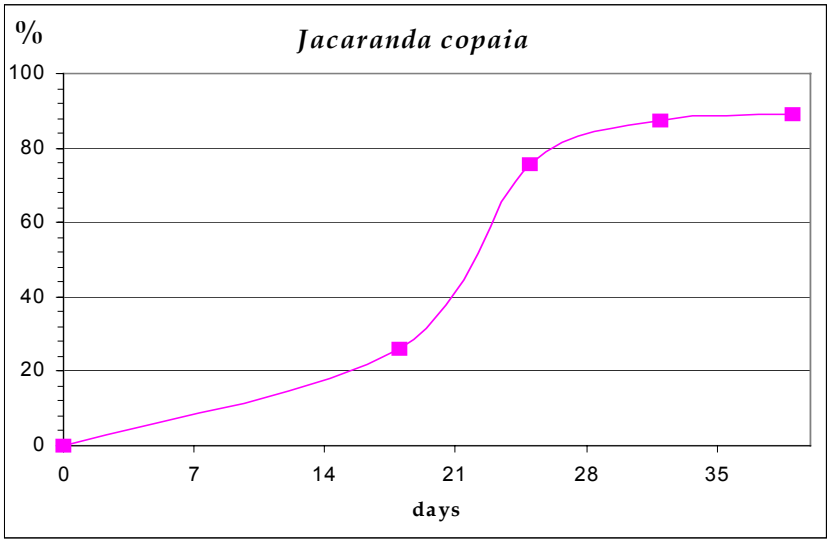

%
Hura crepitans
100
80
60
40
20
0
0
7
14
21
28
35
days

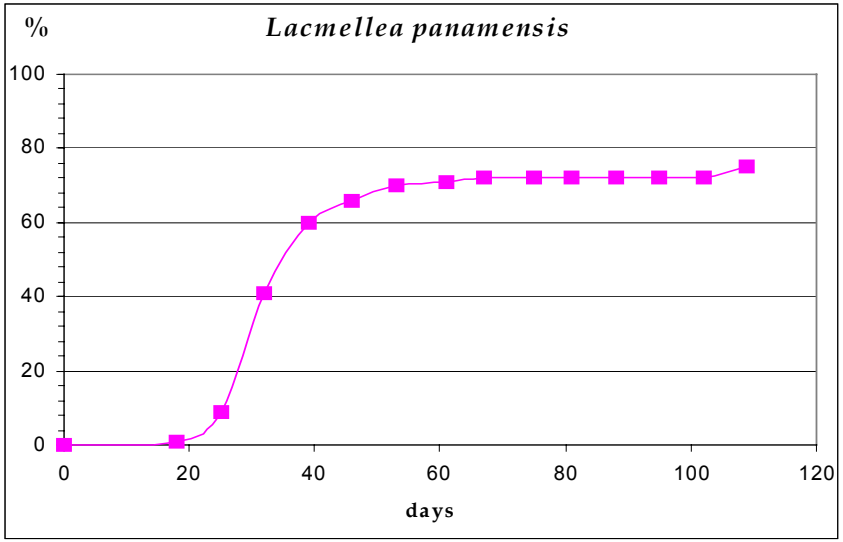

%
Hyeronima alchorneoides
100
80
60
40
20
0
0 15 30 45 60 75 90 105 120 135 150 165
days

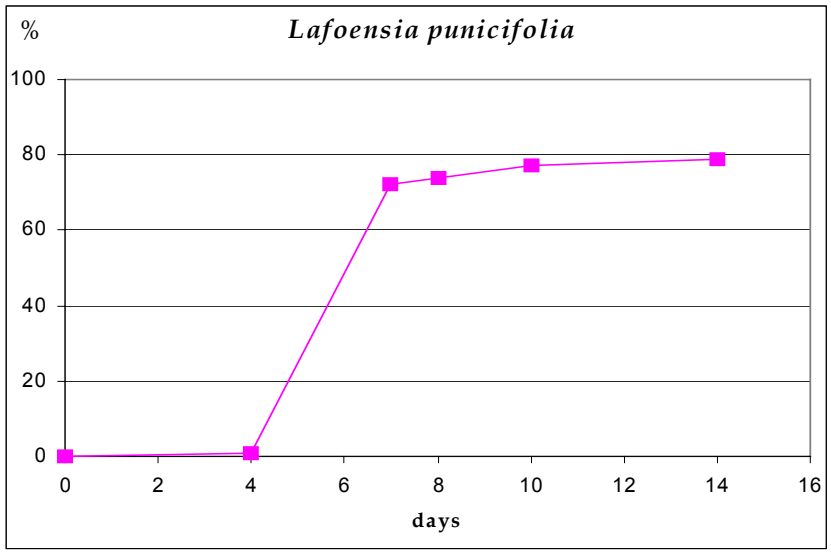

%
Hymenaea courbaril
100
80
60
40
20
0
0 7 14 21 28 35 42 49 56 63
days

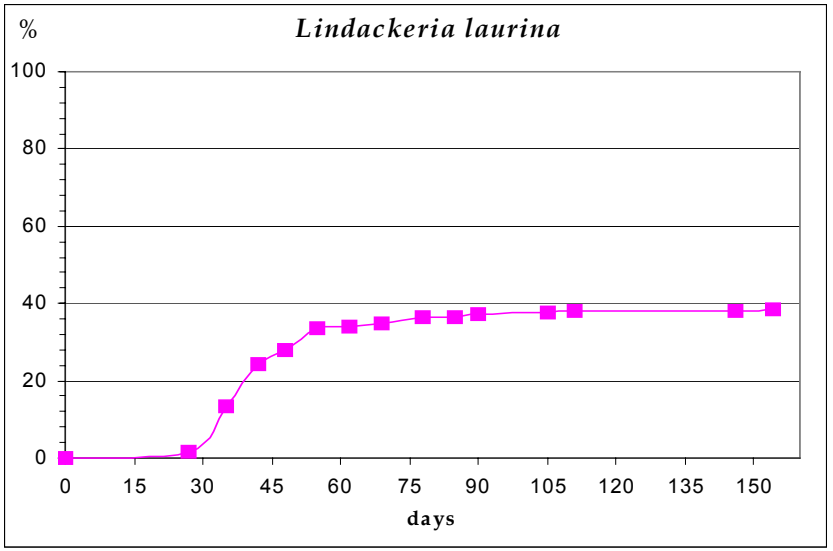

%
Inga punctata
100
80
60
40
20
0
0 7 14 21 28 35
days

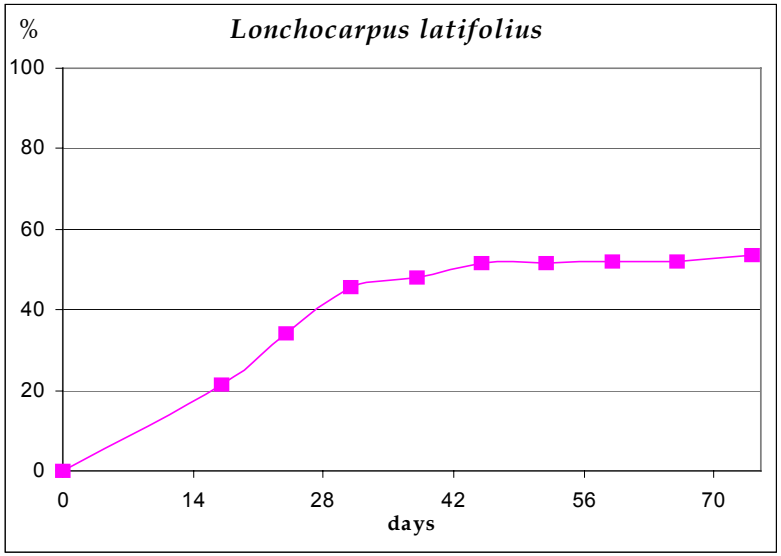

%
Inga spectabilis
100
80
60
40
20
0
0 10 20 30 40 50
days

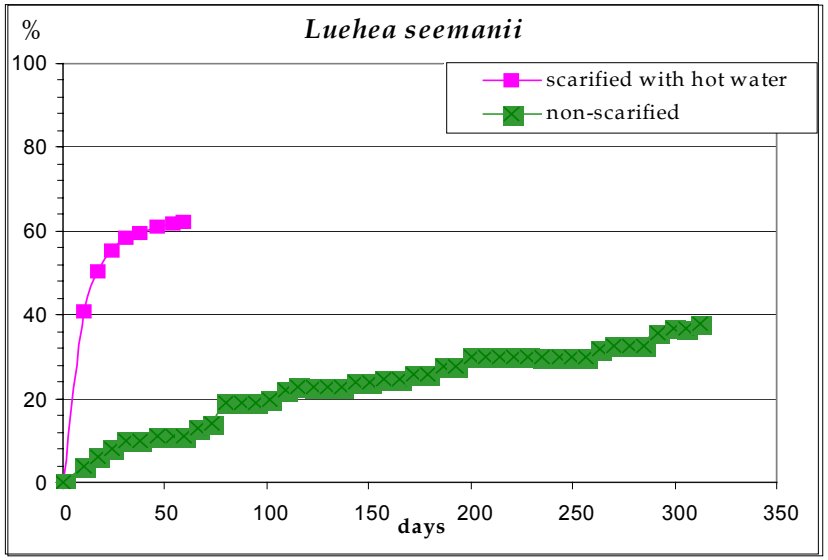

%
Jacaranda copaia
100
80
60
40
20
0
0
7
14
21
28
35
days

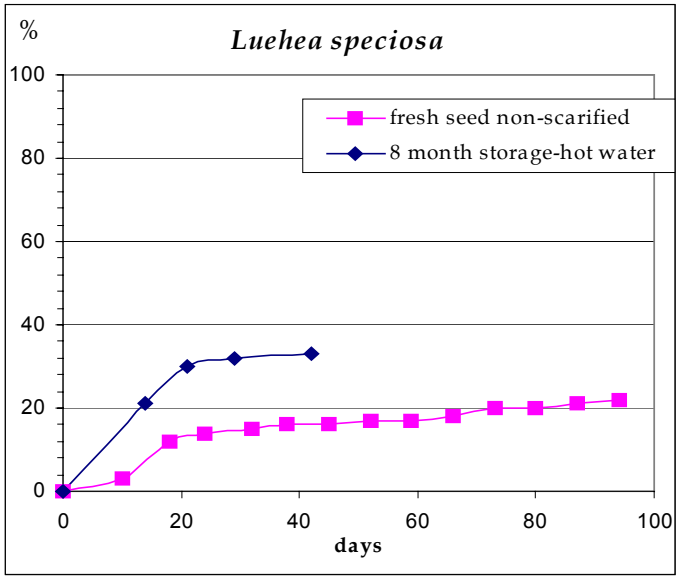

%
Lacmellea panamensis
100
80
60
40
20
0
0
20
40
60
80
100
120
days

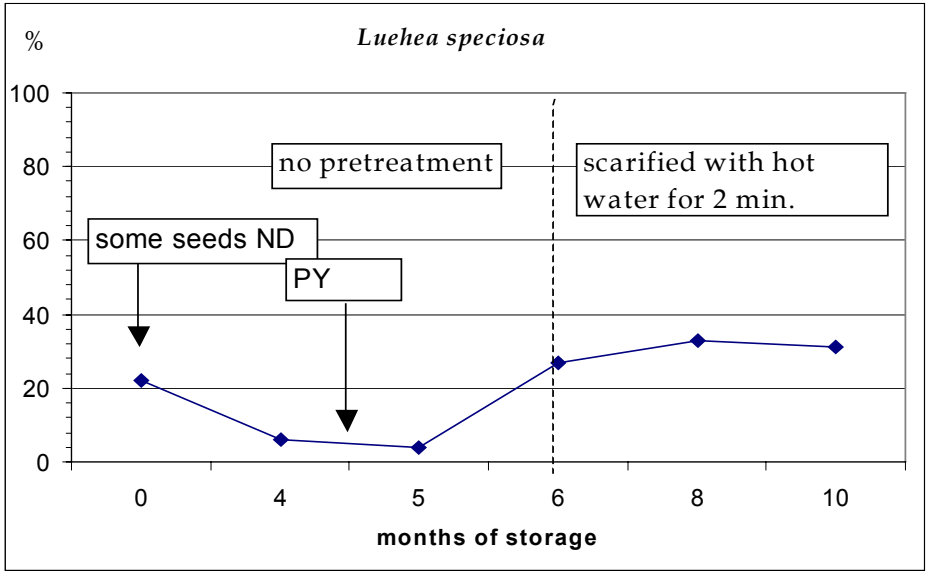

%
Lafoensia punicifolia
100
80
60
40
20
0
0
2
4
6
8
10
12
14
16
days

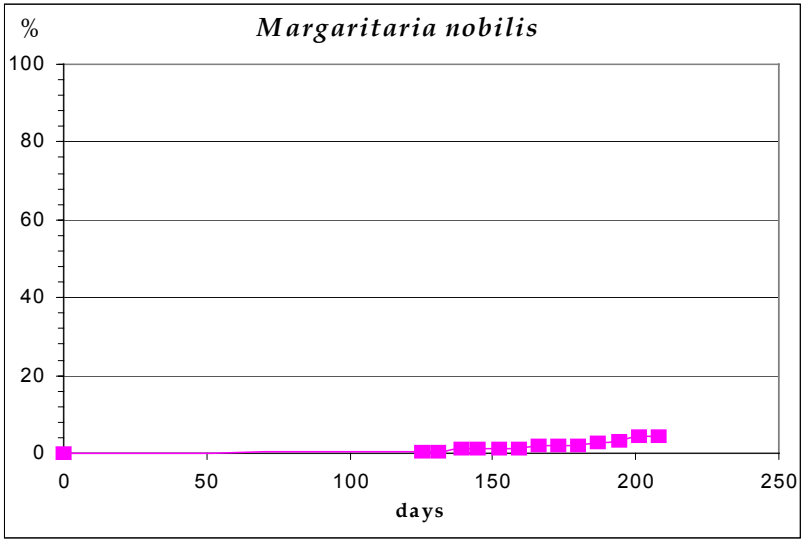

%
Lindackeria laurina
100
80
60
40
20
0
0
15
30
45
60
75
90
105
120
135
150
days

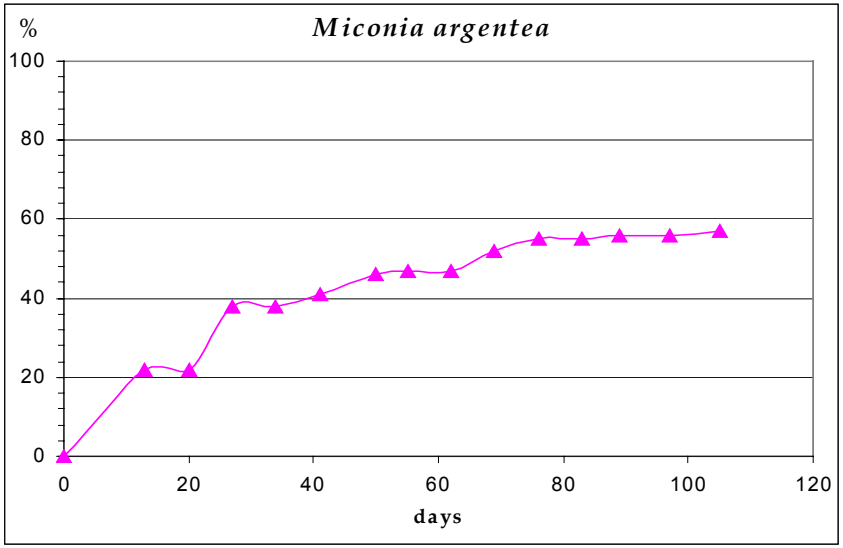

%
Lonchocarpus latifolius
100
80
60
40
20
0
0
14
28
42
56
70
days

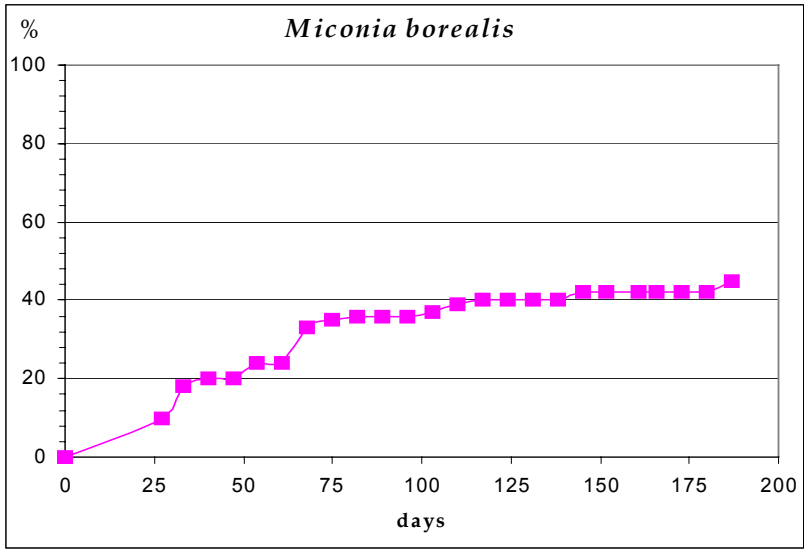

%
Luehea seemanii
scarified with hot water
non-scarified
100
80
60
40
20
0
0
50
100
150
200
250
300
350
days

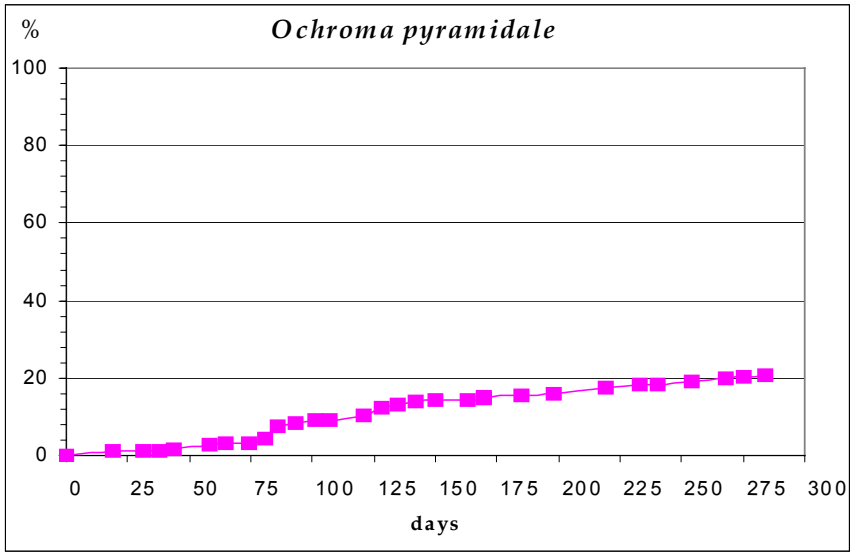

%
Luehea speciosa
fresh seed non-scarified
8 month storage-hot water
100
80
60
40
20
0
0
20
40
60
80
100
days

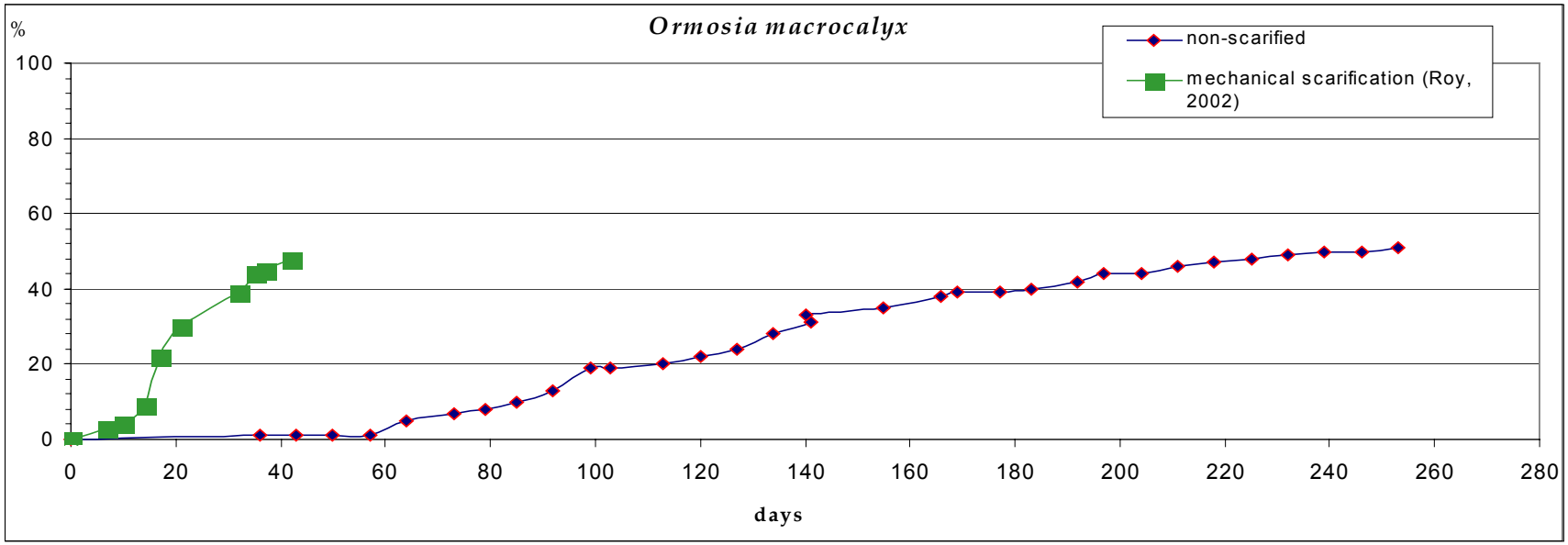

%
Luehea speciosa
no pretreatment
scarified with hot water for 2 min.
some seeds ND
PY
100
80
60
40
20
0
0
4
5
6
8
10
months of storage

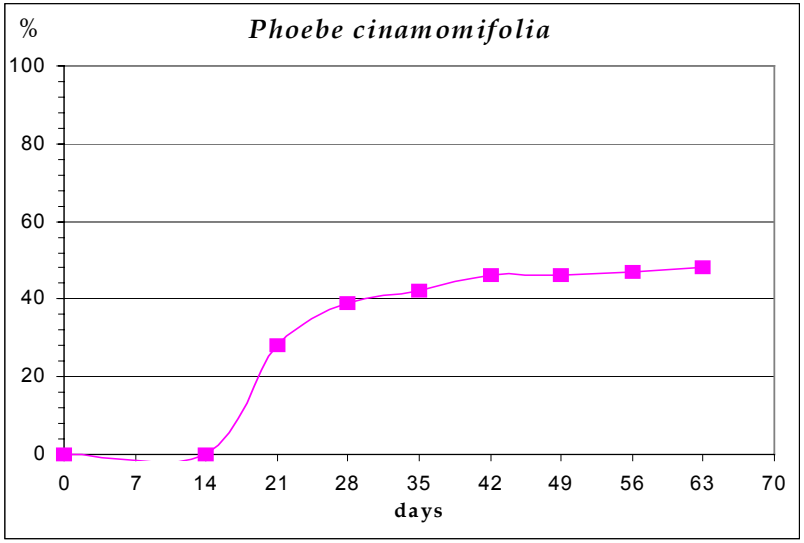

Margaritaria nobilis
%
100
80
60
40
20
0
0
50
100
150
200
250
days

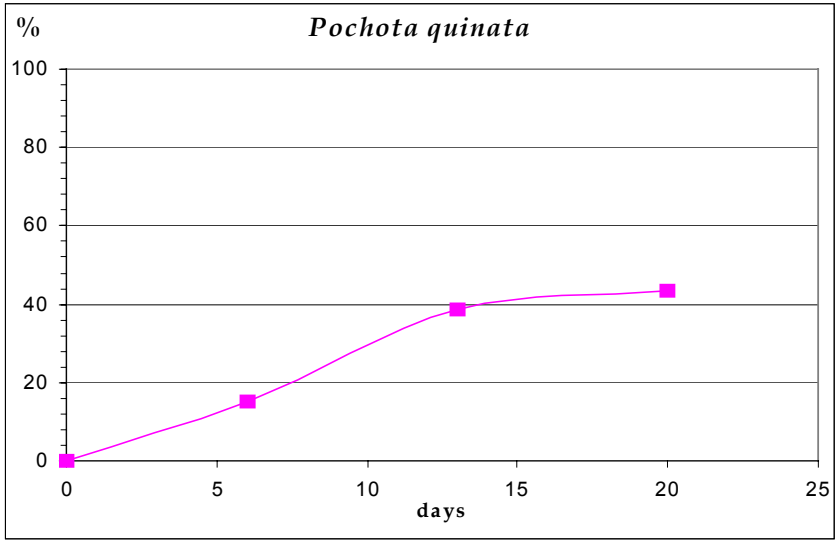

Miconia argentea
%
100
80
60
40
20
0
0
20
40
60
80
100
120
days

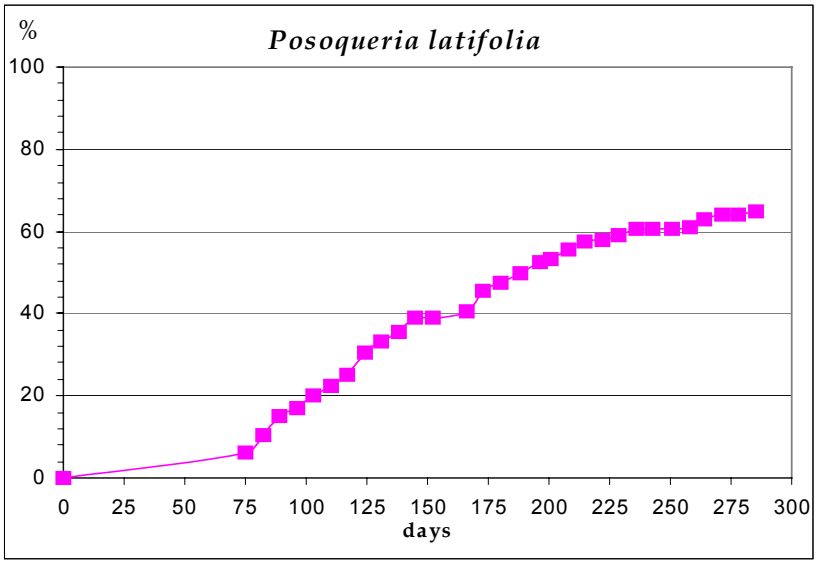

Miconia borealis
%
100
80
60
40
20
0
0
25
50
75
100
125
150
175
200
days

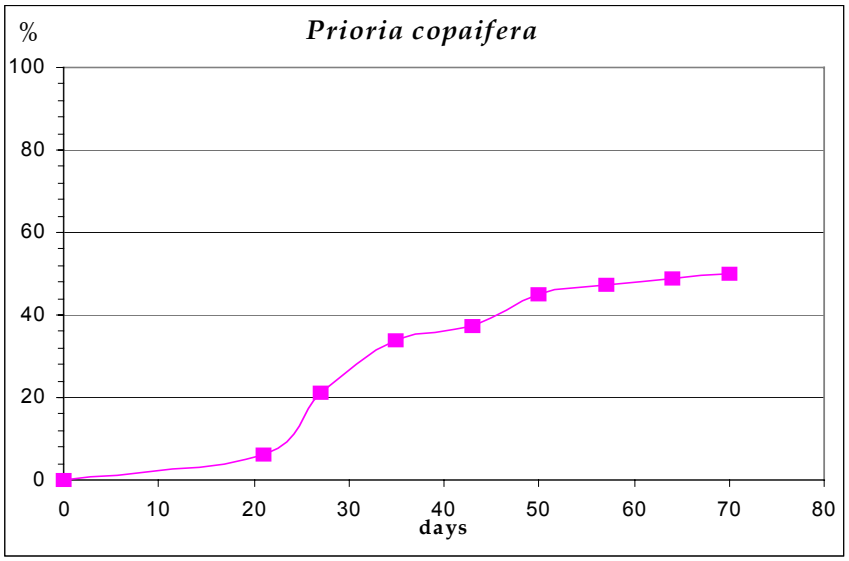

Ochroma pyramidale
%
100
80
60
40
20
0
0
25
50
75
100
125
150
175
200
225
250
275
300
days

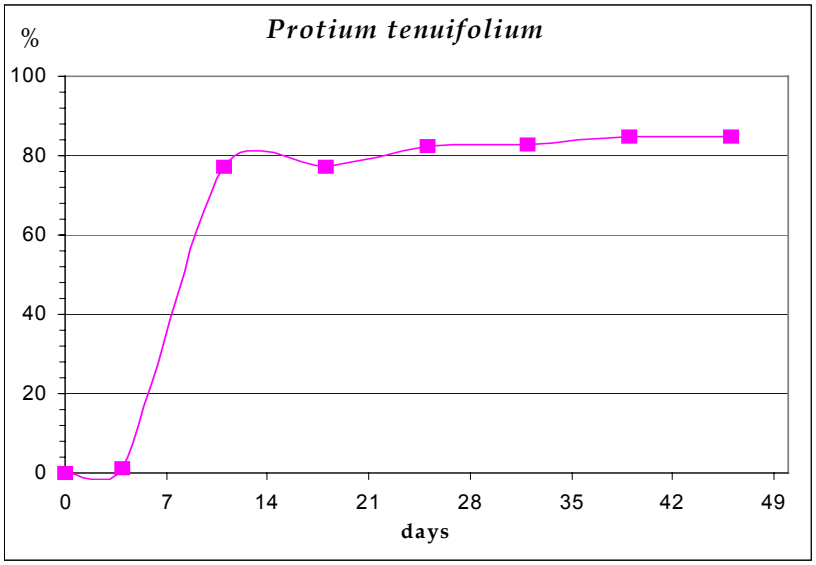

Ormosia macrocalyx
%
100
80
60
40
20
0
0
20
40
60
80
100
120
140
160
180
200
220
240
260
280
days
non-scarified
mechanical scarification (Roy, 2002)

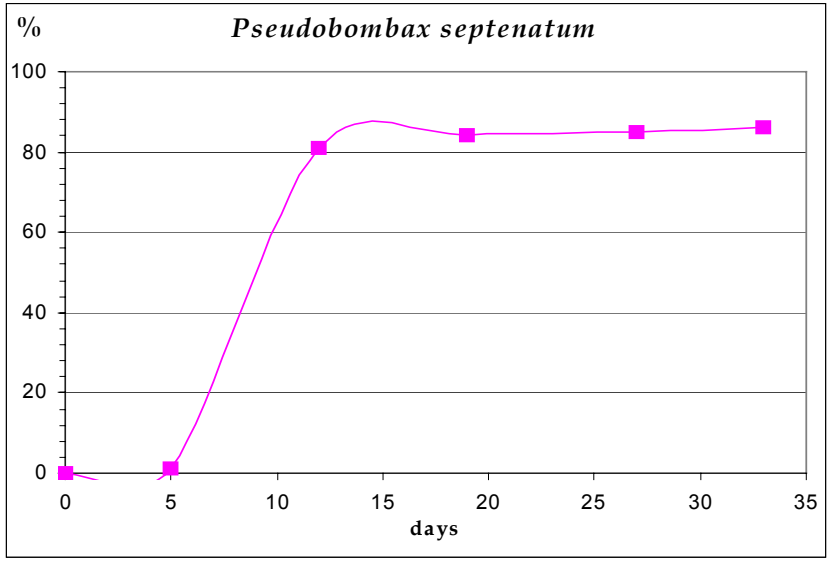

Phoebe cinamomifolia
%
100
80
60
40
20
0
0
7
14
21
28
35
42
49
56
63
70
days

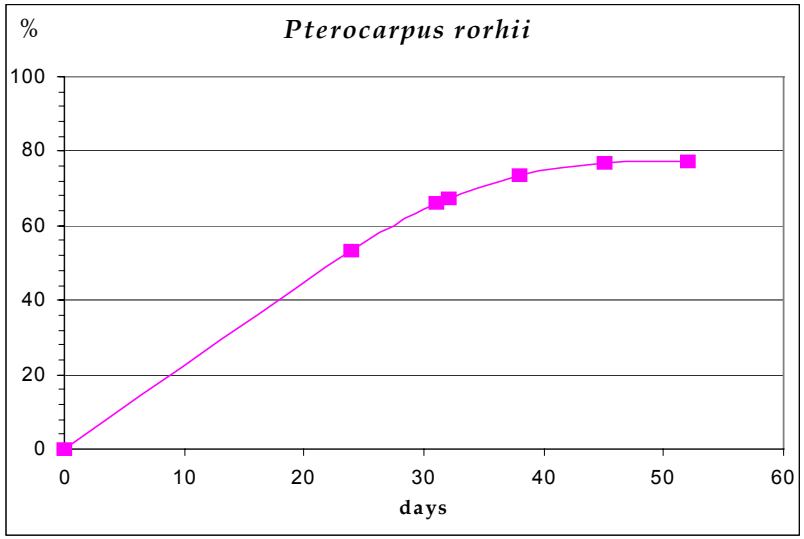

Pochota quinata
%
100
80
60
40
20
0
0
5
10
15
20
25
days

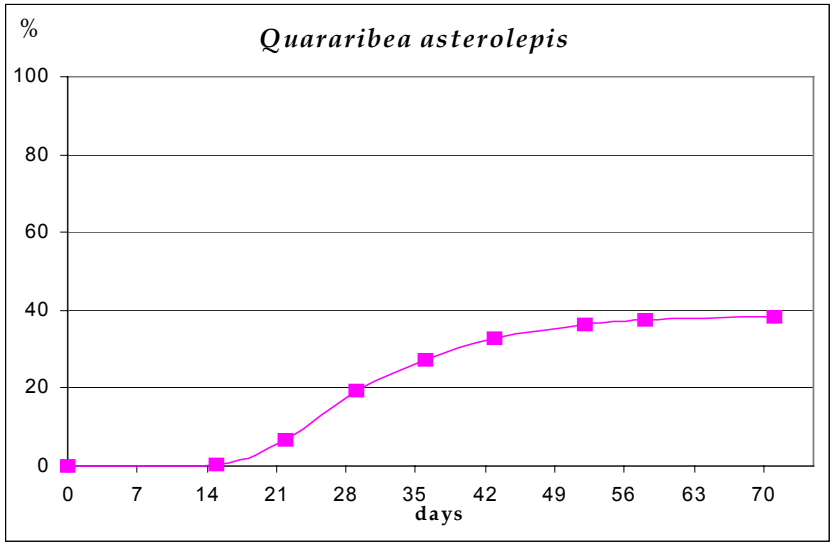

%
Posoqueria latifolia
100
80
60
40
20
0
0 25 50 75 100 125 150 175 200 225 250 275 300
days

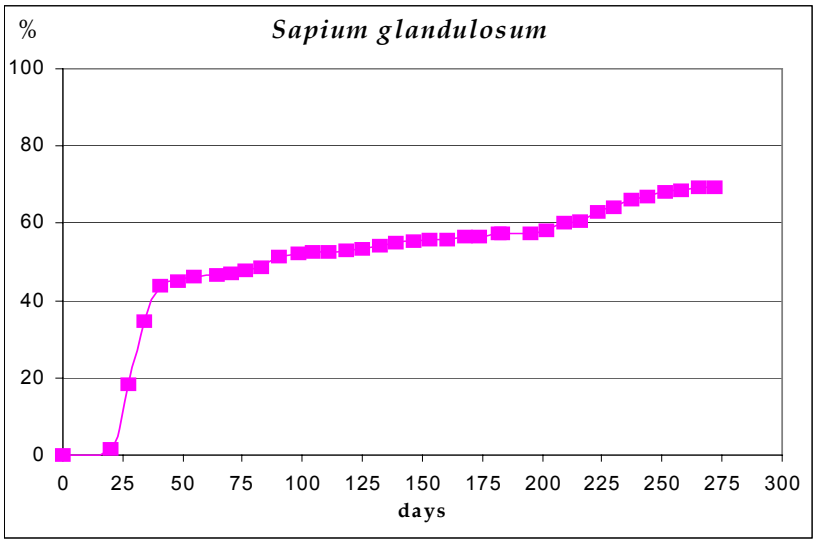

%
Prioria copaifera
100
80
60
40
20
0
0 10 20 30 40 50 60 70 80
days

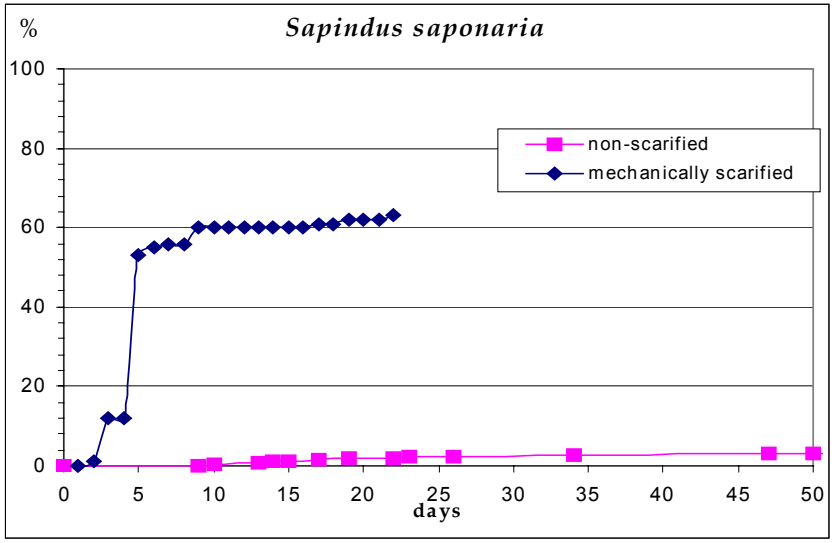

%
Protium tenuifolium
100
80
60
40
20
0
0 7 14 21 28 35 42 49
days

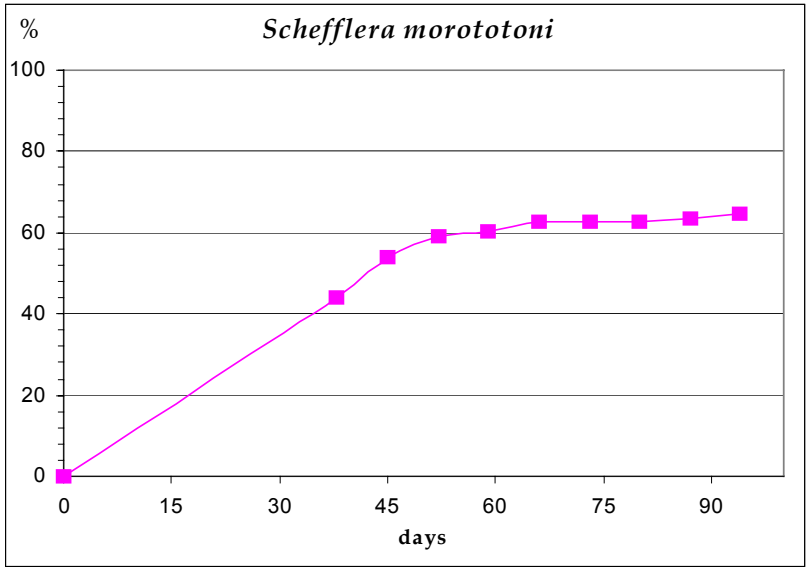

%
Pseudobombax septenatum
100
80
60
40
20
0
0 5 10 15 20 25 30 35
days

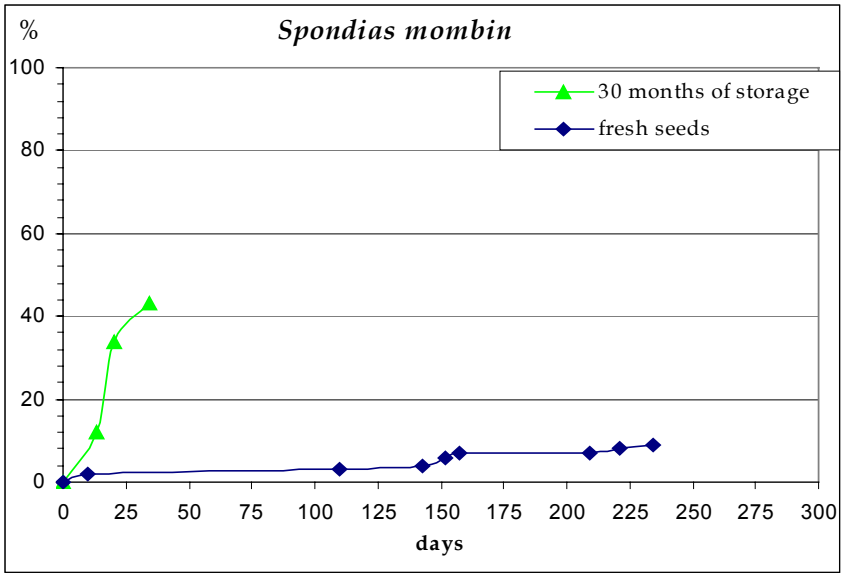

%
Pterocarpus rorhii
100
80
60
40
20
0
0
10
20
30
40
50
60
days

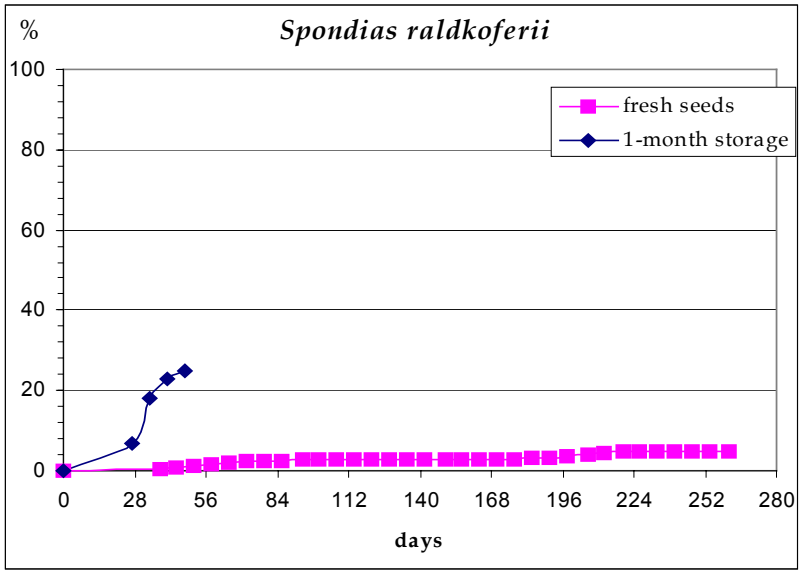

%
Quararibea asterolepis
100
80
60
40
20
0
0
7
14
21
28
35
42
49
56
63
70
days

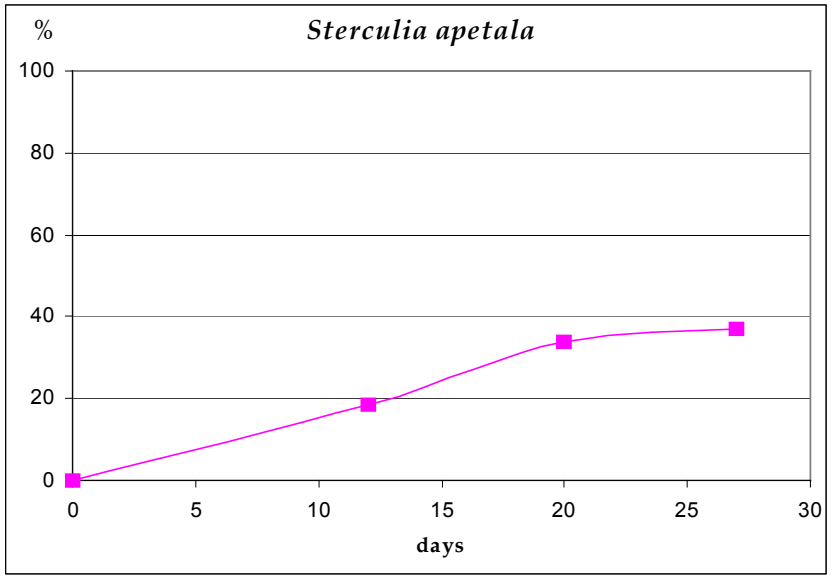

%
Sapium glandulosum
100
80
60
40
20
0
0
25
50
75
100
125
150
175
200
225
250
275
300
days

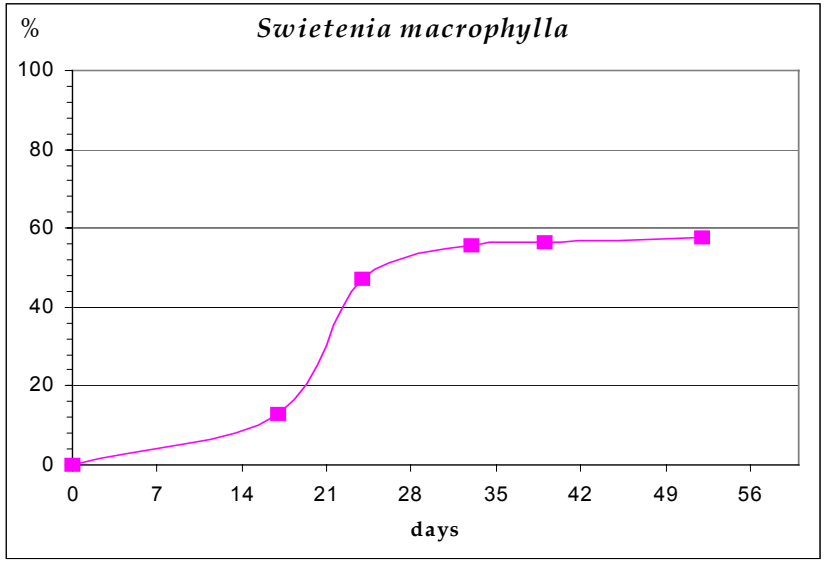

%
Sapindus saponaria
non-scarified
mechanically scarified
100
80
60
40
20
0
0
5
10
15
20
25
30
35
40
45
50
days

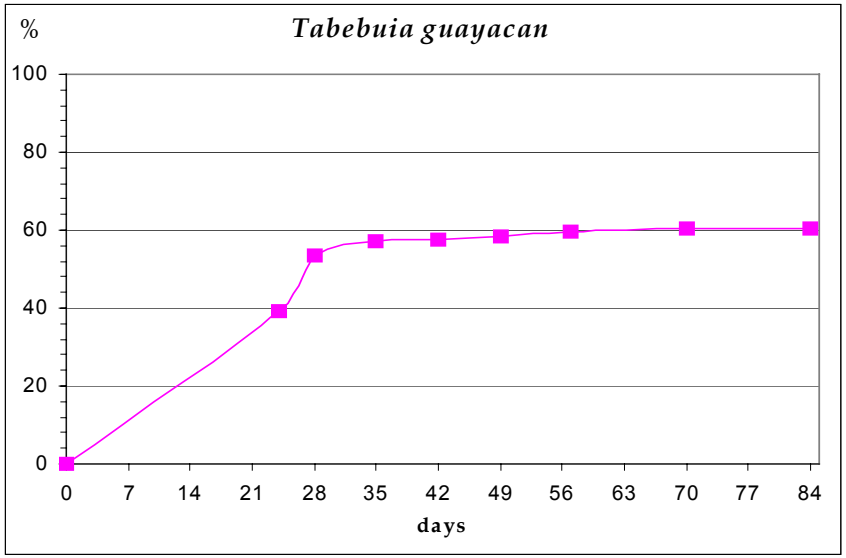

%
Schefflera morototoni
100
80
60
40
20
0
0
15
30
45
60
75
90
days

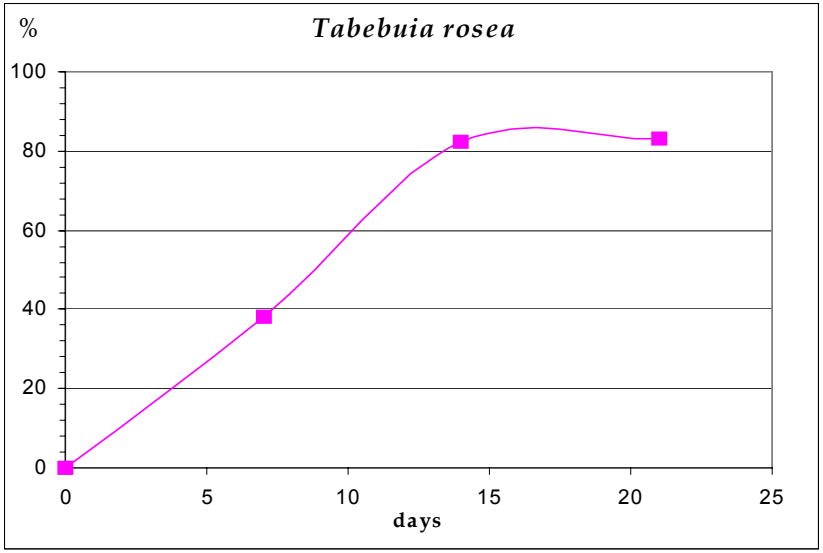

%
Spondias mombin
30 months of storage
fresh seeds
100
80
60
40
20
0
0
25
50
75
100
125
150
175
200
225
250
275
300
days

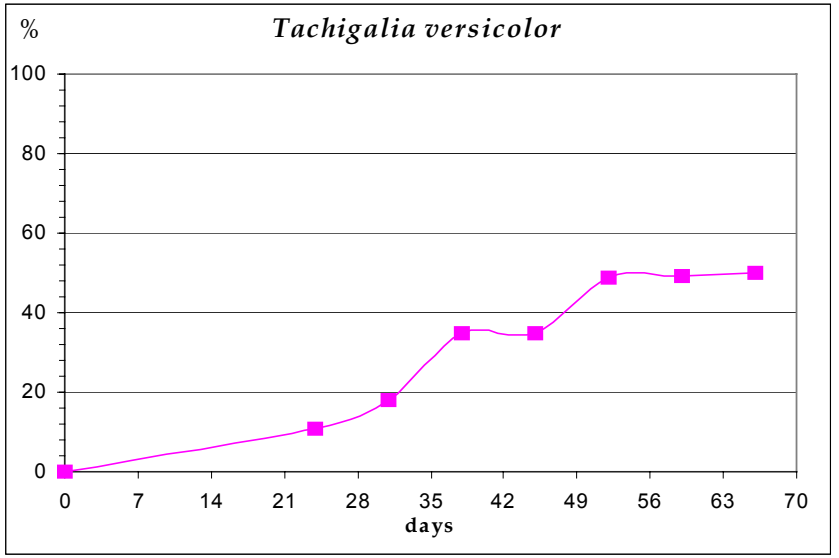

%
Spondias raldkoferii
fresh seeds
1-month storage
100
80
60
40
20
0
0
28
56
84
112
140
168
196
224
252
280
days

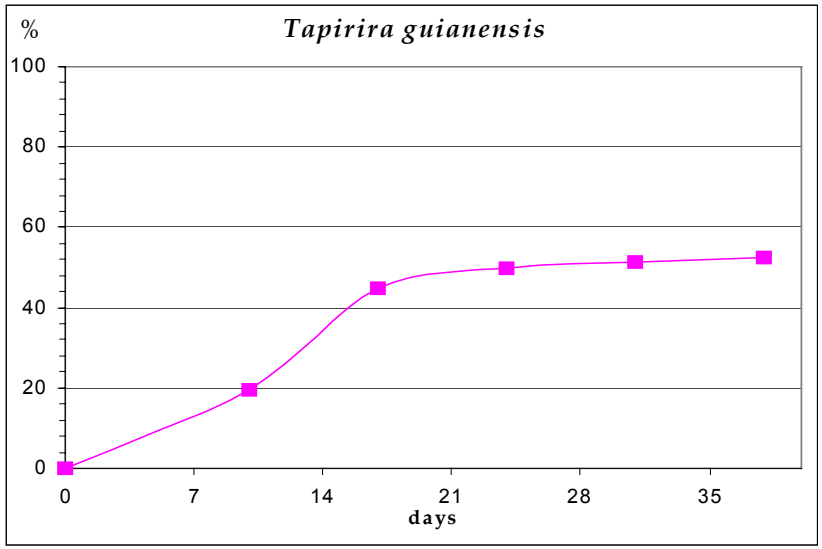

%
Sterculia apetala
100
80
60
40
20
0
0
5
10
15
20
25
30
days

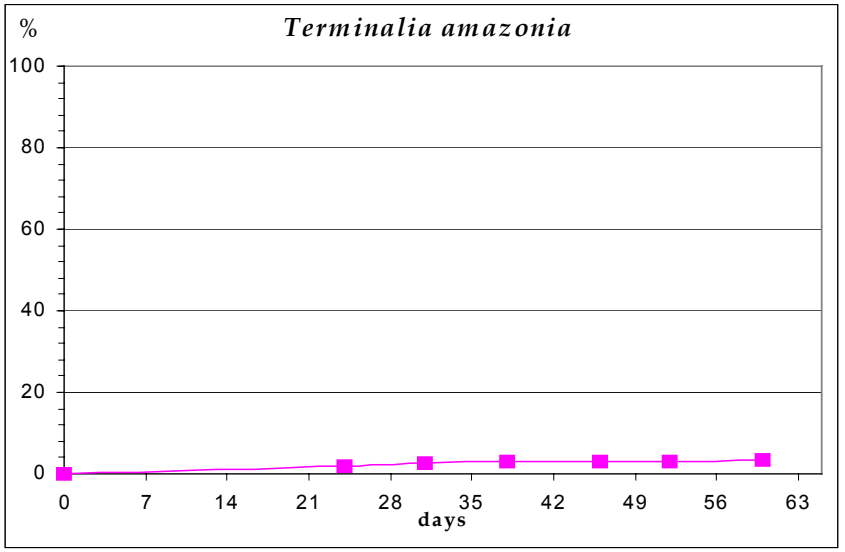

%
Swietenia macrophylla
100
80
60
40
20
0
0
7
14
21
28
35
42
49
56
days

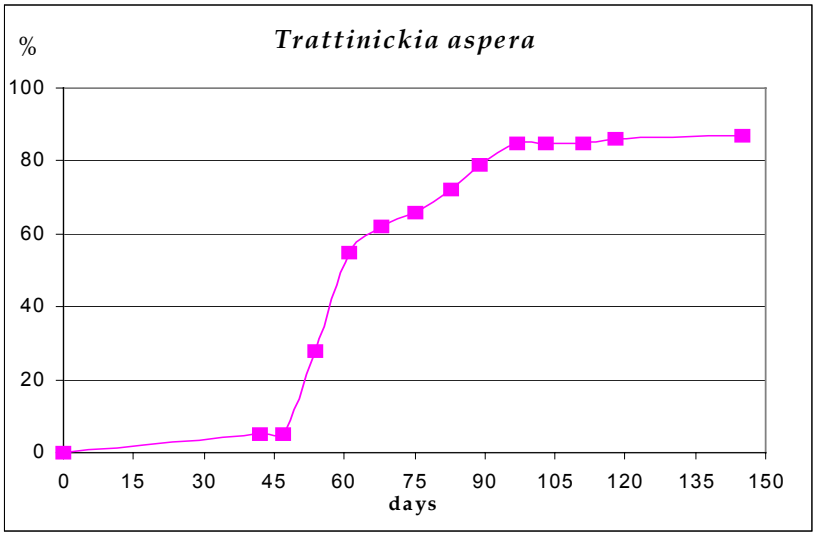

%
Tabebuia guayacan
100
80
60
40
20
0
0
7
14
21
28
35
42
49
56
63
70
77
84
days

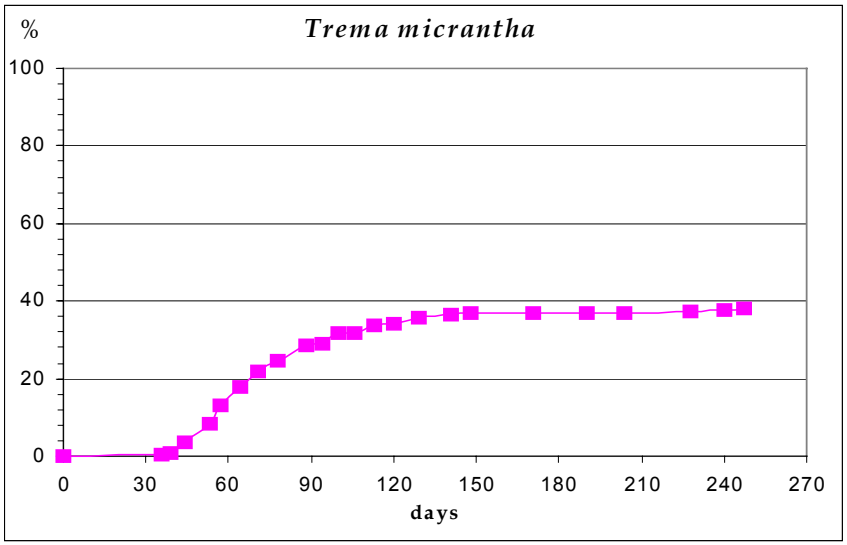

%
Tabebuia rosea
100
80
60
40
20
0
0
5
10
15
20
25
days

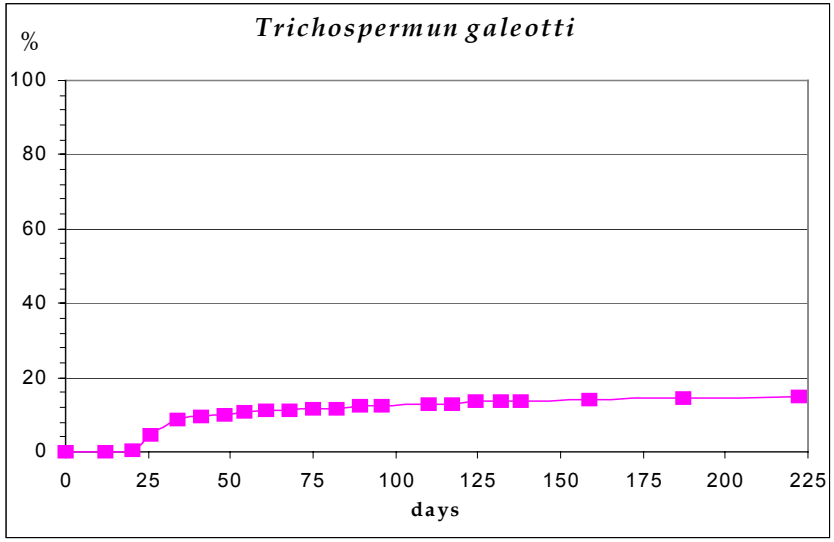

%
Tachigalia versicolor
100
80
60
40
20
0
0
7
14
21
28
35
42
49
56
63
70
days

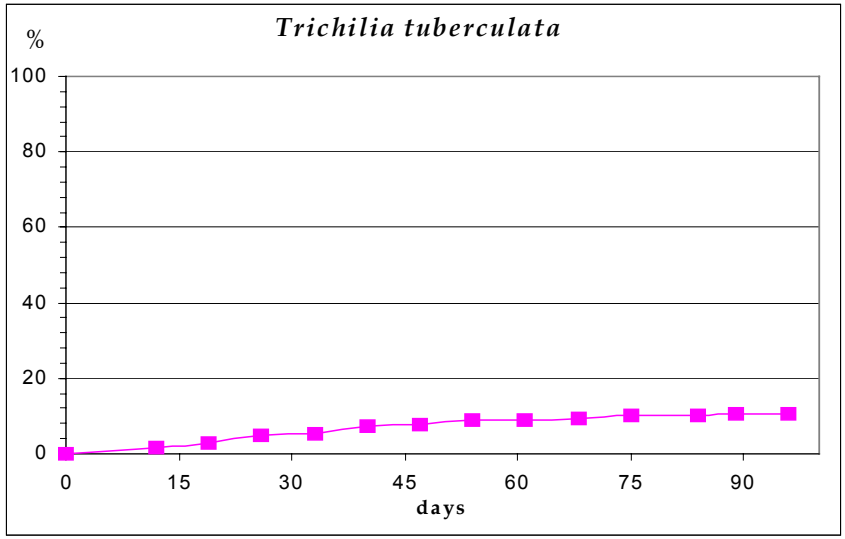

Tapirira guianensis
%
100
80
60
40
20
0
0
7
14
21
28
35
days

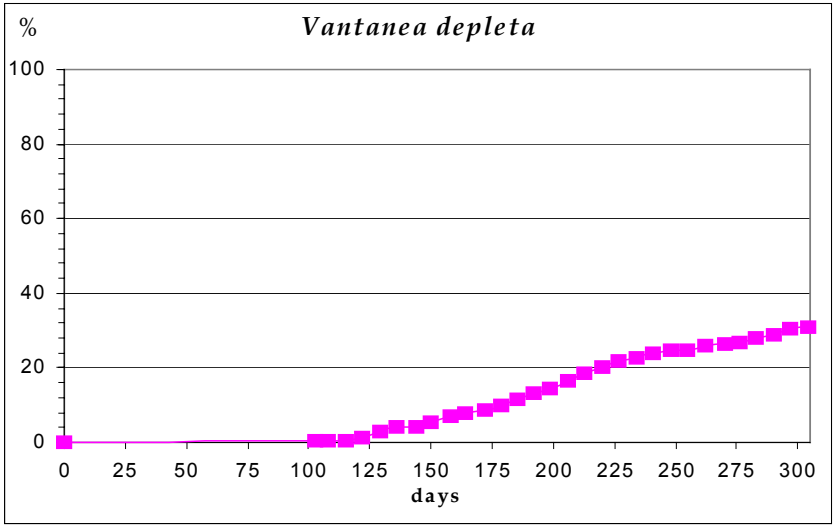

Terminalia amazonia
%
100
80
60
40
20
0
0
7
14
21
28
35
42
49
56
63
days

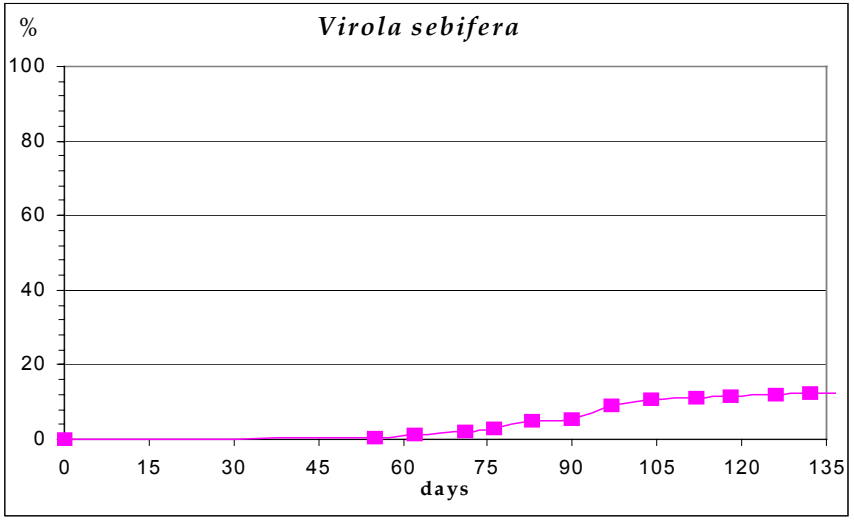

Trattinickia aspera
%
100
80
60
40
20
0
0
15
30
45
60
75
90
105
120
135
150
days

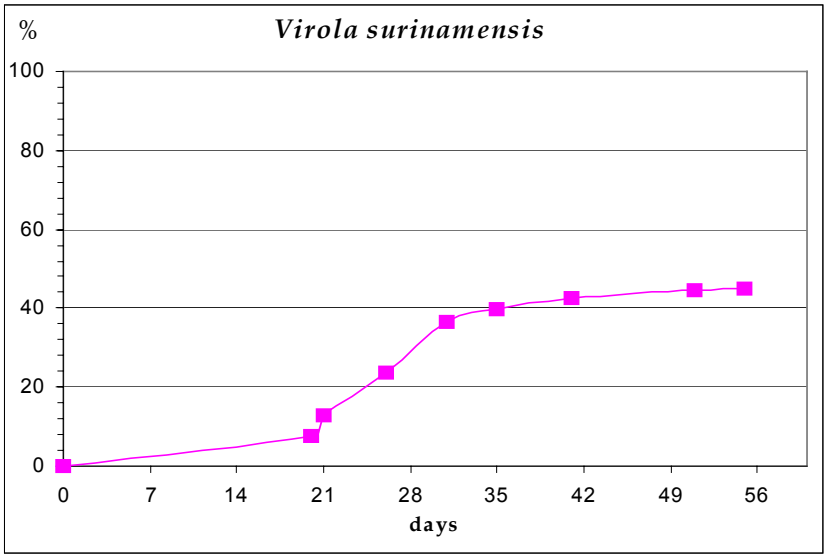

Trema micrantha
%
100
80
60
40
20
0
0
30
60
90
120
150
180
210
240
270
days

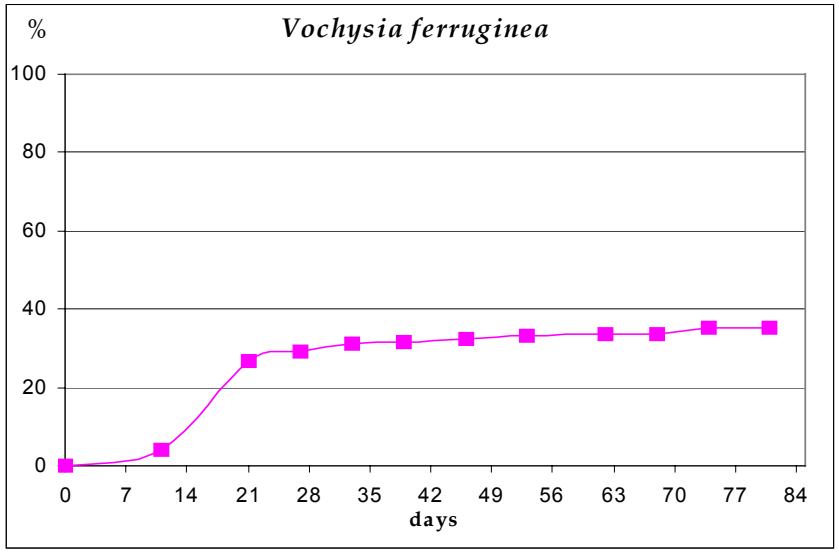

Trichospermun galeotti
%
100
80
60
40
20
0
0 25 50 75 100 125 150 175 200 225
days

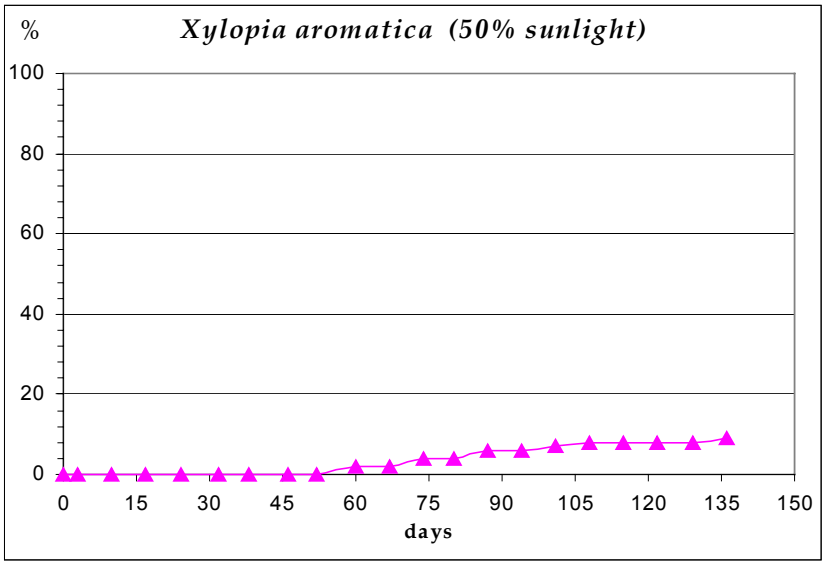

Trichilia tuberculata
%
100
80
60
40
20
0
0 15 30 45 60 75 90
days

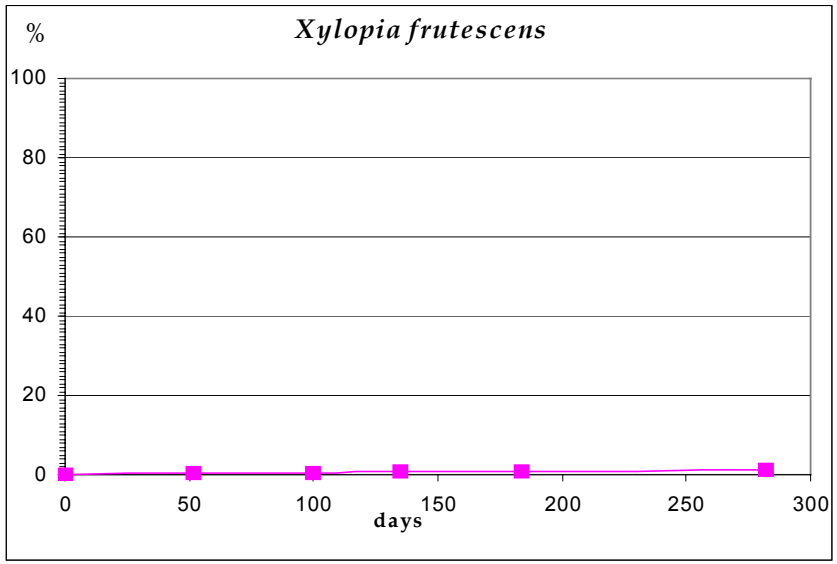

Vantanea depleta
%
100
80
60
40
20
0
0 25 50 75 100 125 150 175 200 225 250 275 300
days


Virola sebifera
%
100
80
60
40
20
0
0 15 30 45 60 75 90 105 120 135
days


%
Virola surinamensis
100
80
60
40
20
0
0
7
14
21
28
35
42
49
56
days


%
Vochysia ferruginea
100
80
60
40
20
0
0
7
14
21
28
35
42
49
56
63
70
77
84
days


%
Xylopia aromatica (50% sunlight)
100
80
60
40
20
0
0
15
30
45
60
75
90
105
120
135
150
days


%
Xylopia frutescens
100
80
60
40
20
0
0
50
100
150
200
250
300
days

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## VITA

Name: **Adriana Sautu**

Born: City Bell, Buenos Aires, Argentina, 14 April 1959.

### Education

Licenciatura. (Biology) – National University of La Plata. Argentina. 1987

### Professional positions held

- Native Species Reforestation Project, Panama. Research Associate 2002-2004
- Native Species Reforestation Project, Panama. Coordinator 2001-2002
- Native tree cultivation in Panama: Collection, germination, viability of seeds, and growing of seedlings of less well-known species, Panama. Coordinator, 1995-2000
- Center for Tropical forest Science, Panama. Research Assistant 1994-1995
- Smithsonian Marine Education Program, Panama, Environmental Educator, 1992-2002
- Biological inventory for the Panama Canal, ANCON-University of Panama Consortium. Field Assistant 1991-1992

### Grants and Fellowships

Tree Seed Dormancy In The Panama Canal Watershed. 2004. **Center for Tropical Forest Grants**. $ 8,000.00. To collect seeds to study tree seed dormancy pattern across a precipitation gradient.

**OEA-FULBRIGHT Grant in Ecology** to complete a Master Degree. 2002-2004. Tuition and living expenses.

Proyecto de Reforestación con Especies Nativas (PRORENA): The Development of Reforestation Strategies for Degraded Landscapes in Panama using Native Species of Trees. 2001-2002. Kennedy School of Government, Harvard University, and Center for Tropical Forest Science. **AVINA Foundation**. $ 30,000. With CTFS, YTRI and CDI.

Bridging STRI's Marine Education Program Activities With the Panamanian Curricula: A Synergistic Approach**.** Smithsonian Tropical Research Institute. With the STRI's Office of Public Programs. 2001-2002. **Smithsonian Outreach Program Grants**. $ 20,000.00. To develop 23 activities specially design for the Environmental Education to use from Kindergarten to K12.

Native Tree Cultivation in Panama: Collect, Germination, Viability of seeds and seedling's growth of less known species. 1996-2000 **Natura Foundation**. $250,000. With Richard Condit.

Biofouling. 1989-1990. **Nacional Council for Scientific and Technological Research, Argentina**. Fellowship for the beginning researchers Living expenses.

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